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**A MONOGRAPHIC STUDY OF RANUNCULUS
SUBGENUS BATRACHIUM (DC.) A. GRAY**

by

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Introduction

Ranunculus subgenus *Batrachium* was not granted any virtues by the older herbalists and probably for this reason was not often mentioned in their works. In spite of this, HIERN (1871) discovered some 75 pre-Linnaean names. Most species of *Ranunculus* are poisonous but the batrachia are non-toxic and may even be of some value as fodder since PULTENY (1798) reports having fed them to some horses, cows and pigs for a whole year; about the pigs he said "Hogs are also fed with the same plant on which they improve so well, that it is necessary to allow them other sustenance, 'till it is proper to put them up to fatten". In general, however, the batrachia have no economic importance except, perhaps, to some water conservancy boards and fishermen who find them troublesome weeds.

The batrachian ranunculi have been considered a "difficult group" for a long time and in consequence have attracted many workers. This difficulty doubtless stems from the extreme degree of phenotypic plasticity exhibited by many species. In 1753 LINNAEUS recognised 5 taxa (2 species and 3 varieties). After 10 years work I now recognise 20 taxa for the world for which, to date, I have discovered 302 available names and combinations of names from which to choose. The choice has not been easy. Figure 1 is a histogram illustrating the accumulation of new names and combinations of names per decade that are assignable to the two Linnaean species. This histogram follows, fairly closely, the equal distribution curve and reflects well the rise and fall of "alpha" or descriptive taxonomy within this group.

There have been many local monographs and revisions of *Ranunculus* subgenus *Batrachium*. Excluding accounts in Floras, the most significant are: LAWSON (1884), DAVIS (1900), DREW (1936) and BENSON (1948, 1954) for North America, LOURTEIG (1952, 1956) for South America, MEIKLE (1959) for the Orient, ROSSMANN (1854) and GLÜCK (1924, 1936) for most of Europe, DUMORTIER (1863), FREYN (1890) and FÉLIX (1910, 1911, 1912, 1913, 1914, 1925, 1926, 1927) for West Europe, SCHILLER (1918) for Hungary, TULLBERG (1873) and GELERT (1894) for Scandinavia and BABINGTON (1855, 1856, 1878) and PEARSALL (1921, 1928) for the British Isles.

HIERN (1871) made the only attempt at a world monograph.

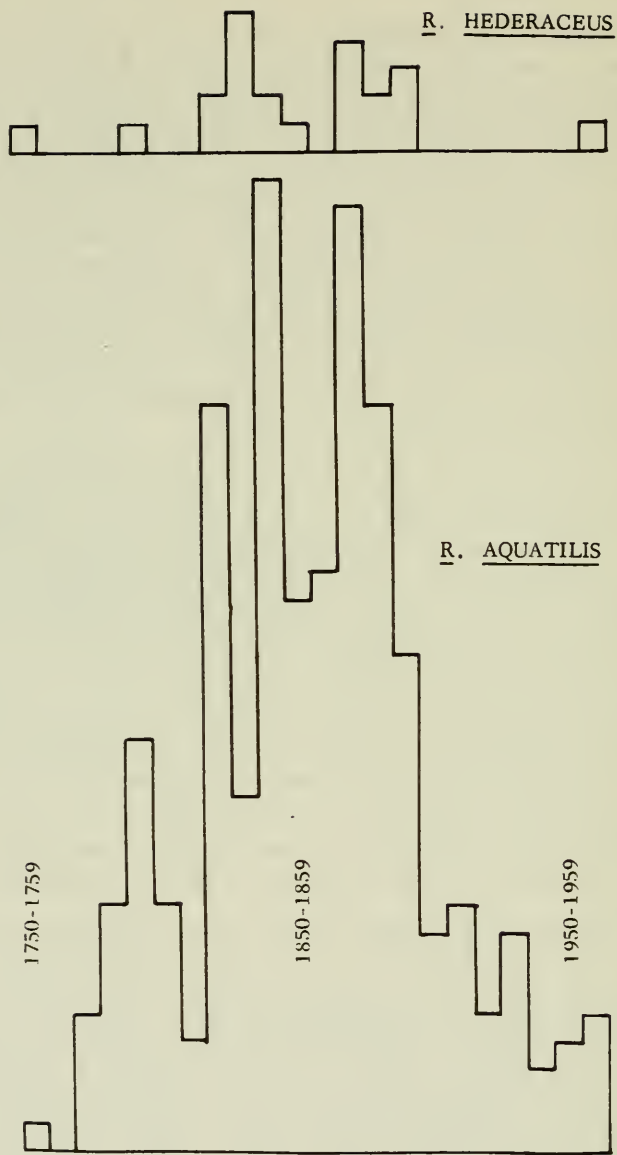


Fig. 1.: New names and combinations of names per decade that are assignable to the two Linnaean species.

He cultivated a few species and realised that there was considerable phenotypic variation in the group. In order, he thought, to avoid greater confusion he recognised only one species (*R. hydrocharis*) and assigned to it 35 "ultimate forms". About these ultimate forms he said, "They must not be considered as generally equivalent to subspecies; in many cases, at least, their characters depend upon purely external or accidental causes and the plants are not genetically distinct. On the other hand, some forms retain their characters through very diverse circumstances, and they can, for many purposes, be regarded as true species." HIERN determined many herbarium specimens at Kew (K) and the British Museum (BM) and I have found his work very valuable. Unfortunately, his "ultimate forms" are illegitimate according to the Code of Botanical Nomenclature (1961) as they have no definite taxonomic rank. I have, however, included them in the synonymy of the appropriate taxa.

Most of the above workers have relied almost entirely on herbarium studies. One notable exception, however, was GLÜCK (1924) who cultivated nearly all the European species and studied their reaction to desiccation, depth of water and seasonal changes. He chose the taxonomic ranks "forma" and "subforma" for phenotypic modifications and he divided each species he studied more or less arbitrarily into several formae and subformae. This usage of the categories forma and subforma finds little favour to-day but, in spite of this, GLÜCK'S work remains very valuable. Unfortunately, his personal herbarium was destroyed during the 1939-1945 war but I have seen many herbarium specimens determined by him at München (M) and I am confident that I have interpreted his occasionally inadequate descriptions correctly. GLÜCK'S work has not gone unrecognised and it is notable that most post-1930 European Floras recognise fewer species of *Batrachium*.

While too many taxonomists may have worked on this group too little attention has been paid to it by morphologists, physiologists and geneticists. *R. aquatilis* appears in many standard botanical textbooks as an example of a heterophyllous plant but ASKENASY (1870) appears to be the only person to have seriously investigated heterophylly in this species although he was more interested in the development and structure of the different kinds of leaves than in factors governing their production. GESSNER (1940) studied the effects of carbon dioxide and light intensity on the leaf development of *R. baudotii* and WILSON (1947) and MORTLOCK (1952) attempted to study the transpiration stream

in *R. penicillatus* var. *calcareus* (misidentified as *R. fluitans* in their work). None of this work, unfortunately, has contributed to the systematics of this group. SALISBURY (1934, 1960) carried out some biometrical work on a few wild populations of three species but within each species he was unable to detect any inter-population variation. Apart from a few chromosome counts, I have not discovered any genetical work on *Batrachium*.

I first began studying *Batrachium* in the summer of 1956 at Cambridge University under the supervision of Dr. WALTERS who initially persuaded me to work on this group. Studies were continued at the Universities of München and Liverpool. At the beginning, most of my time was spent collecting wild plants and studying their reactions to different environmental conditions in cultivation. Along with this work cytological, embryological and morphological investigations were undertaken and breeding experiments were carried out. As my knowledge of phenotypic variation patterns increased, herbarium studies were undertaken in order to find geographical distributions and local variations.

I have attempted to describe the group on a world-wide basis. In this revision I recognise 17 species and have been very fortunate in having 14 of them in cultivation. My concept of species in this group has largely been dictated by the plants themselves. Some species are "good" in the sense that they are morphologically, genetically and ecologically distinct while others are "bad" in the sense that they are not distinct. The delimitation of "bad" species is not simply a taxonomic problem; they are bad because they are genetically heterogeneous. To-day there are known to be many mechanisms controlling genetic variability in plant populations. It is sometimes possible to understand or, perhaps, interpret the genetical situation at the population level but it is often difficult to fit the plants themselves into a formal taxonomic framework.

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Materials and Methods

The work reported in this study was carried out from August 1956 to March 1960 at the University of Cambridge, from April 1960 to August 1961 at the University of München and from October 1961 to the present time at the University of Liverpool. Field work was carried out in the British Isles during the years 1956 - 1960. During 1960 and 1961 field work was undertaken in Holland, Germany, Austria, Switzerland, Italy and Sicily and from 1961 to the present in the British Isles.

About 10,000 herbarium specimens have been examined from the following herbaria:

BIRM	The University, Birmingham, England.
BM	British Museum (Natural History), London, England.
BR	Jardin Botanique de l'Etat, Bruxelles, Belgium.
C	Botanical Museum and Herbarium, Copenhagen, Denmark.
CGE	Botany School, University of Cambridge, England.
COI	Botanical Institute of the University, Coimbra, Portugal.
E	(non-British Material) The Royal Botanic Garden, Edinburgh, Scotland.
G	(Orient material only) Conservatoire et Jardin Botaniques, Genève, Switzerland.
K	Royal Botanic Gardens, Kew, England.
LD	Botanical Museum and Herbarium, Lund, Sweden.
LE	Botanical Institute, Academy of Sciences, Leningrad, USSR.
LIV	City Museums, Liverpool, England.
LIVU	Hartley Botanical Laboratories, University of Liverpool, England.
M	Botanische Staatssammlung, München, Germany.
MANCH	The Manchester Museum, Manchester, England.
NAP	Erbarii dell'Orto Botanico dell'Università, Napoli, Italy.
W	Naturhistorisches Museum, Wien, Austria.

I have endeavoured to attach determinavit or confirmavit labels to all herbarium specimens examined. At the time of writing, this is incomplete in the following herbaria: BM, COI, K, LE, MANCH and NAP.

The following is a list of the origins of living plant material that has been maintained in cultivation for six months or more:

R. hederaceus

- H-1. Sellindge, Hythe, Kent, England. Coll. O. R. Staples, 28 September 1956.
- H-2. Ponsongath, The Lizard, Cornwall, England. Coll. C. D. K. Cook, 30 March 1958.
- H-3. synthesized autotetraploid of H-2, September 1958.
- H-4. Mora, Alto Alentejo, Portugal. Coll. B. V. Rainha, 12 June 1958.
- H-5. Eifel, Stadtkyll, Prüm, Germany. Coll. D. Podlech, 25 May 1961.
- H-6. Penrhos Lligwy, Angelsey, Wales, Coll. C. D. K. Cook, 13 May 1962.
- H-7. Bwlch-y-Rhiw, Aberdaron, Caernarvonshire, Wales. Coll. C. D. K. Cook, 14 May 1962.
- H-8. Porthmynawyd, Pembroke, Wales. Coll. J. J. Gill, April 1964.

R. omiophyllus

- Om-1. Abbots Moss, Marton, Cheshire England. Coll. K. Goodway, 8 March 1957.
- Om-2. Wistman's Wood, Two Bridges, Dartmoor, Devon, England. Coll. C. D. K. Cook, 4 May 1958.
- Om-3. Polizzi Generosa, Madonie Mts., Sicily. Coll. C. D. K. Cook, 21 April 1961.

R. tripartitus

- Tp-1. Kynance, The Lizard, Cornwall, England. Coll. C. D. K. Cook, 21 March 1957.
- Tp-2. Ponsongath, The Lizard, Cornwall, England. Coll. C. D. K. Cook, 22 March 1957.

- Tp-3. Arne, Dorset, England. Coll. C. D. K. Cook,
24 March 1957.
- Tp-4. Kynance, The Lizard, Cornwall. Coll. D. E.
Coombe, April 1964.
- Tp-5. Arne, Dorset, England. Coll. E. M. Burrows,
April 1964.

R. ololeucos

- Ol-1. Maarn, Utrecht, Holland. Coll. C. D. K. Cook &
T. W. J. Gadella, 1 April 1960.

R. baudotii

- B-1. Frampton Marsh, Boston, Lincolnshire, England.
Coll. C. D. K. Cook, 15 August 1956.
- B-2. On the saltmarsh at Brading, Isle of Wight, England.
Coll. C. D. K. Cook, 20 May 1958.
- B-3. Zick See, St. Andrat-Frauenkirchen, Burgenland,
Austria. Coll. C. D. K. Cook & A. Patzak,
26 June 1960.
- B-4. Krokbyströmmen, Gennarbyviken, Tenala, Regio
aboënsis, Finland. Coll. H. Luther, 3 July 1961.

R. saniculifolius

- Sa-1. Prastio, Cyprus. Coll. D. Meikle, No. 618,
May 1962.

R. peltatus

- Pl-1. Madeley, Staffordshire, England. Coll. K. W.
Goodway, 11 June 1956.
- Pl-2. Pant-y-rhiw, Radnorshire, Wales. Coll. F.
Perring, 12 August 1956.
- Pl-3. Seed from Coimbra Botanic Garden, Portugal.
Received March 1957.
- Pl-4. Holmsley, Brockenhurst, Hampshire, England.
Coll. C. D. K. Cook, 19 May 1958.

- Pl-5. Hatchett Pond, Beaulieu, Hampshire, England.
Coll. C. D. K. Cook, 19 May 1958.
- Pl-6. Casa Bravea, Portugal. Coll. J. Poelt, 4 June 1959.
- Pl-7. Slayley Moor, Bonsall, Derbyshire, England.
Coll. C. D. K. Cook, 9 July 1959.
- Pl-8. between Erlangen and Dechsendorf, Hoechstadt,
Unterfranken, Germany. Coll. C. D. K. Cook &
D. Podlech, 17 September 1960.
- Pl-9. between Carmona and La Lusiana, Sevilla, Spain.
Coll. J. Poelt, 3 April 1961.

R. penicillatus var. penicillatus

- Pna-1. River Fane, Dundalk, County Louth, Eire.
Coll. D. A. Webb, 1 June 1957.
- Pna-2. River Elz, Prechtal, Pfalz, Germany. Coll.
C. D. K. Cook, 8 June 1960.

R. penicillatus var. calcareus

- Pnb-1. Puddletown, Dorset, England. Coll. C. D. K.
Cook, 31 March 1958.
- Pnb-2. River Wye, Haddon, Derbyshire, England.
Coll. C. D. K. Cook, 22 May 1959.
- Pnb-3. Foulmere, Cambridgeshire, England. Coll.
C. D. K. Cook, 17 June 1959.
- Pnb-4. Oberlaus, Glonn, Bavaria, Germany. Coll.
C. D. K. Cook, 30 May 1960.
- Pnb-5. Sigmaringen, Württemberg, Germany. Coll.
C. D. K. Cook, 7 June 1960.

R. penicillatus var. vertumnus

- Pnc-1. Greywell, Hampshire, England. Coll. C. D. K.
Cook, 24 June 1958.

R. sphaerospermus

- Sp-1. between Qurna and Madina, Iraq. Coll.
K. H. Rechinger fil., 17 March 1957 (No. 8477).

R. aquatilis

- A-1. Stow Woods, Buckinghamshire, England.
Coll. F. Perring, 22 May 1956.
- A-2. Bretby Ponds, Repton, Derbyshire, England.
Coll. C. D. K. Cook, 15 August 1956.
- A-3. Castle Donington, Leicestershire, England.
Coll. C. D. K. Cook, 20 August 1956.
- A-4. Barton Pond, Cambridge, Cambridgeshire, England.
Coll. S. M. Walters, 1956, November 1956.
- A-5. Predannik, The Lizard, Cornwall, England.
Coll. C. D. K. Cook, 22 March 1957.
- A-6. Roadside ditch about 2 km south of Stretham,
Cambridgeshire, England. Coll. C. D. K. Cook,
1 May 1957.
- A-7. Woodwalton Fen, Huntingdonshire, England.
Coll. C. D. K. Cook, 1 May 1959.
- A-8. Tuddenham, Suffolk, England. Coll.
C. D. K. Cook, 12 May 1959.
- A-9. Markeaton Brook, Quorndon, Derbyshire, England.
Coll. C. D. K. Cook, 22 May 1959.
- A-10. Pöcking, Starnberg, Oberbayern, Germany.
Coll. C. D. K. Cook, 1 June 1960.
- A-11. Erling, Herrsching, Oberbayern, Germany.
Coll. C. D. K. Cook, 26 August 1960.
- A-12. Formby Moss, Southport, Lancashire, England.
Coll. C. D. K. Cook, May 1964.

R. trichophyllus subsp. trichophyllus

- Tt-1. Adventurer's Fen, Wicken, Cambridgeshire,
England. Coll. C. D. K. Cook, 20 September 1956.
- Tt-2. Stoer, Sutherland, Scotland. Coll. C. D. K. Cook,
August 1958.
- Tt-3. Cressbrook, Monsal Dale, Derbyshire, England.
Coll. C. D. K. Cook, 26 March 1957.

- Tt-4. Woodwalton Fen, Huntingdonshire, England.
Coll. C. D. K. Cook, 7 May 1959.
- Tt-5. River Würm, Obermenzing, München, Germany.
Coll. C. D. K. Cook, 30 May 1960.
- Tt-6. Ascholding, Oberbayern, Germany. Coll.
C. D. K. Cook, 25 May 1960.
- Tt-7. 1.5 km S. W. of Oberstdorf, Allgäu, Germany.
Coll. C. D. K. Cook, 9 August 1960.
- Tt-8. Fischen, Allgäu, Germany. Coll. C. D. K. Cook,
10 August 1960.
- Tt-9. Polizzi Generosa, Madonie Mts., Sicily.
Coll. C. D. K. Cook, 21 April 1961.
- Tt-10. Martigny-Ville, Vallais, Switzerland.
Coll. C. D. K. Cook, 30 May 1961.

R. trichophyllus subsp. lutulentus

- Tl-1. Funtensee, Berchtesgadener Alpen, Germany.
Coll. C. D. K. Cook, 17 July 1960.
- Tl-2. Geissalpsee, Allgäuer Alpen, Germany. Coll.
C. D. K. Cook & W. Gutermann, 8 August 1960.
- Tl-3. Mjosund, Oja, Ostrobothnia media, Finland.
Coll. H. Luther, 30 July 1961.

R. rionii

- R-1. Maqil, Basra, Iraq. Coll. K. H. Rechinger fil.,
16 March 1957 (No. 15808).
- R-2. Hyair, Iraq. Coll. K. H. Rechinger fil.,
17 March 1959 (No. 8488a).
- R-3. Prater, Wien, Austria. Coll. C. D. K. Cook &
A. Patzak, 24 June 1960.
- R-4. Himberg, Mannswörth, S. E. Austria.
Coll. C. D. K. Cook, 25 June 1960.

R. circinatus

- C-1. Hemington, Leicestershire, England.
Coll. C. D. K. Cook, 15 August 1956.

- C-2. Cheddar, Somerset, England. Coll.
H. K. Whitehouse, 26 March 1957.
- C-3. Woodwalton Fen, Huntingdonshire, England.
Coll. C. D. K. Cook, 7 May 1959.
- C-4. The Lode at Wicken Fen, Cambridgeshire,
England. Coll. C. D. K. Cook, 2 June 1959.
- C-5. Oberlaus, Glonn, Oberbayern, Germany.
Coll. C. D. K. Cook, 10 June 1960.
- C-6. Nymphenburger Kanal, München, Germany.
Coll. C. D. K. Cook, 20 July 1960.

R. fluitans

- F-1. The Lode, Wicken Fen, Cambridgeshire,
England. Coll. C. D. K. Cook, August 1956.
- F-2. Markeaton Brook, Quorndon, Derbyshire,
England. Coll. C. D. K. Cook, 11 June 1957.
- F-3. River Lark, Temple Bridge, Tuddenham, Suffolk,
England. Coll. C. D. K. Cook, 19 June 1958.
- F-4. Whatstandwell, Derbyshire, England.
Coll. C. D. K. Cook, 18 June 1959.
- F-5. Schleissheimer Kanal, Dachau, München, Germany.
Coll. C. D. K. Cook, 25 May 1960.
- F-6. Donaueschingen, Württemberg, Germany.
Coll. C. D. K. Cook, 9 June 1960.

R. omiophyllus X tripartitus

- NH-1. Holmsley, Brockenhurst, Hampshire, England.
Coll. C. D. K. Cook, 19 May 1958.

R. aquatilis X trichophyllus

- NH-2. Woodwalton Fen, Huntingdonshire, England.
Coll. C. D. K. Cook, 7 May 1959.

R. fluitans X peltatus

- NH-3. Peakirk, Northamptonshire, England. Coll.
C. D. K. Cook, 19 June 1959.

R. fluitans X trichophyllus or aquaticus

NH-4. Monsal Dale, Derbyshire, England. Coll.
C.D.K. Cook, 3 June 1959

R. fluitans X trichophyllus

NH-5. River Würm, Obermenzing, München, Germany.
Coll. C.D.K. Cook, 30 May 1960.

At the University of Cambridge Botanic Garden, the following eight "standard" environments were set up:

1. Water-logged soil	] unshaded]	outdoors
2. 25 cm deep water		
3. 100 cm deep water		
4. 150 cm deep water		
5. Flowing water		
6. 25 cm deep water	] shaded]	in a cool but frost-free green-house
7. Water-logged soil		
8. 25 cm deep water		

Except in special cases the plants were grown in pots in John Innes No. 1 potting mixture and stood in tanks of water. The water used in the standard environments was obtained from a well in Cambridge Botanic Garden. Flowing water was obtained by pumping water along a narrow trough; the pump used produced approximately 240 litres per minute and it was possible to maintain a flow of approximately 30 cm per second over plants if they were kept small.

Ramets of the following wild collected plants were kept in these eight standard environments for uninterrupted periods of at least 3 months: H-1, H-2, H-3, H-4, Om-1, Om-2, Tp-1, Tp-2, B-1, B-2, Pl-3, Pl-4, Pna-1, Pnb-1, Pnb-2, Pnb-3, Pnc-1, A-3, A-6, Tt-1, Tt-3, C-1, C-2, C-4, F-1, F-2, F-3, NH-1, NH-3, NH-4. The following were kept in standard environments 2, 3, 7 or 8: Tp-3, Pl-5, Pl-7, Pnb-3, A-1, A-2, A-5, A-7, A-8, A-9, Tt-2, Tt-4, C-3, F-4, NH-2.

During 1960 and 1961 at München, plants were cultivated under more or less uniform conditions in 50 cm of water in concrete tanks outdoors or cultivated terrestrially in a cool but frost-

free greenhouse. Ramets of the following plants were maintained for at least 6 months: H-2, H-3, H-5, Om-2, Om-3, Tp-1, Ol-1, B-2, B-3, Pl-3, Pl-6, Pl-8, Pna-2, Pnb-4, Pnb-5, Sp-1, A-6, A-10, A-11, Tt-1, Tt-5, Tt-6, Tt-7, Tt-8, Tt-9, Tt-10, Tl-1, Tl-2, R-1, R-2, R-3, R-4, C-4, C-5, C-6, F-5, F-6, NH-5.

From 1961 to the present at Liverpool, plants have been cultivated under more or less uniform conditions in 1 m or 25 cm of water in concrete tanks or cultivated terrestrially in a cool but frost-free greenhouse. Ramets of the following plants have been maintained for at least 6 months: H-2, H-3, H-5, H-6, H-7, H-8, Om-2, Om-3, Tp-1, Tp-4, Tp-5, Ol-1, B-2, B-3, B-4, Sa-1, Pl-3, Pl-6, Pl-8, Pl-9, Pnb-1, A-6, A-12, Tt-1, Tt-7, Tt-9, Tl-3, R-3, C-4.

Throughout the ten years' study, many herbarium specimens have been made. These specimens and the raw data from my original measurements will, for the time being, be retained by me. The results obtained from the cultivation experiments are summarized in the section on the evaluation of taxonomic characters and in the sections on variation that accompany the description of each species. Special techniques or experimental procedures are described in the text where appropriate.

I have delimited species morphologically because I have found that it is the only practical method. Within some of the species so delimited there are genetic barriers, but they can only be detected by applying genetic techniques. These intra-specific genetic barriers are important from an evolutionary point of view and are described in the text, but the genetically-isolated components are not assigned to any formal taxonomic category. The category subspecies is only used once and applies to a morphologically distinct, ecologically separated vicariant that may have had a polytopic origin. The category varietas is used for morphologically distinct segmental amphidiploids.

The synonymy following each species contains all the names I have found that apply to that species; many of the synonyms are invalid, but I feel they are nevertheless worth inclusion.

The distribution maps, except where stated, are based on herbarium specimens that I have seen. Unfortunately, in many areas of the world, this method reflects the distribution of collectors rather than that of the plant species.

General Features

All species are annual or perennial herbs. Seed germination is epigeal and the pericarp is often carried above the ground on the cotyledons. The cotyledons are ovate, glabrous and with an entire margin. The length of the hypocotyl is variable and depends upon the depth of water and light intensity. A branching primary root system is formed but adventitious roots arise at the first foliar node. The primary root system and hypocotyl are soon lost after growth of the secondary root system.

Branching is sympodial in all species. During the vegetative phase of *R. hederaceus*, *R. omiophyllus* and *R. tripartitus* the branching may be unequal and regular series of long and short internodes make the plants appear to be opposite-leaved. Flowers are solitary and terminate the growth of the main axis.

Annual or perennial habit

The expression of the annual or perennial habit is largely under environmental control and the situation found in nature is often very different from that found under cultivation. *R. rionii*, *R. sphaerospermus*, *R. saniculifolius* and some strains of *R. peltatus* are obligate annuals in nature and in cultivation. *R. hederaceus*, *R. omiophyllus*, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus*, *R. aquatilis* and *R. trichophyllus* subsp. *trichophyllus* are frequently annual in nature but perennial when cultivated under suitable conditions without competing species. *R. fluitans*, *R. penicillatus* and *R. circinatus* are normally perennial but behave as annuals if cultivated terrestrially. *R. trichophyllus* subsp. *lutulentus*, an arctic-alpine, is perennial in nature but annual if cultivated in temperate conditions.

R. saniculifolius shows marked determinate growth: the stems develop no adventitious roots after the first two nodes. The other annual species are monocarpic but detached vegetative portions will develop roots and can be maintained for more than one year in cultivation. The stems of *R. baudotii*, *R. peltatus* and *R. aquatilis* in the entire-leaved phase are monocarpic while floating or submerged but develop roots and show indeterminate growth when raised above the water surface.

Ecological classification

R. hederaceus and *R. omiophyllus* are primarily terrestrial plants of wet places, and can be described as tenagophytes following the ecological classification of aquatic plants by HEJNÝ (1960). In nature, all other species have a submerged phase during their generative history and can be termed hydatophytes. *R. trichophyllus*, *R. rionii*, *R. longirostris*, *R. sphaerospermus*, *R. flavidus*, *R. fluitans*, *R. circinatus* and some strains of *R. penicillatus* and *R. aquatilis* can only exist in a terrestrial state under a regime of long photoperiods but are normally submerged aquatics with emergent generative organs and fall into the sub-group euhydatorphytes. All other species are heterophyllous with vegetative parts that normally come into contact with the air so they are described as hydatoaerophytes. *R. baudotii*, *R. peltatus* and some strains of *R. aquatilis* and *R. penicillatus* develop entire leaves that are confined to the air-water interface while *R. tripartitus*, *R. lobbii*, *R. ololeucos* and *R. saniculifolius* develop entire leaves that may occupy the air-water interface or become fully emergent.

Discussion and Evaluation of Taxonomic Characters

Heterophylly

Many species of *Ranunculus* subgenus *Batrachium* develop two quite different kinds of leaf, one has an expanded, continuous lamina and will be called an "entire" leaf while the other has a lamina of branching, capillary segments and will be called a "divided" leaf.

In most aquatic plants that develop both divided and entire leaves the change from one kind to the other is gradual with the formation of several sequential intermediate leaves. In the heterophyllous species *R. lobbii*, *R. tripartitus*, *R. ololeucos*, *R. baudotii*, *R. peltatus*, *R. penicillatus* and *R. aquatilis* the change in leaf-form is abrupt with a fully divided leaf followed immediately by a normal, fully expanded entire leaf. In aquatics, this abrupt leaf-change is, I believe, confined to *Batrachium* and *Cabomba*. Other aquatic species of *Ranunculus* not in subgenus *Batrachium* such as *R. polyphyllus* Waldst. & Kit. ex Willd., *R. gmelinii* DC. and *R. flabellaris* Raf. develop divided, intermediate and entire

leaves.

The heterophyllous habit in *Batrachium* has received a good deal of attention but many interpretations have been confused by somewhat misdirected teleological thinking. DODOENS (1578), LAMARCK (1809), MER (1880), HENSLOW (1908) and many others have regarded the production of divided leaves as a direct and immediate plastic response to a submerged environment. ROSSMANN (1854) and ASKENASY (1870) discovered that the direct effect of submergence in water alone was sometimes insufficient to change the leaf-form; ARBER (1920) interpreted these findings as heteroblastic development in the sense of GOEBEL (1897).

It is not possible to make many generalizations about heterophylly in *Batrachium* as a whole as each species shows a different reaction. This is not surprising when one considers their general ecology; for example, *R. tripartitum* is essentially terrestrial with a dominant entire-leaved phase, while *R. aquatilis* is essentially aquatic with a short-lived, floating, entire-leaved phase. Therefore each species will be considered separately.

R. aquatilis

The first seedling leaf of *R. aquatilis* is always divided at any time of the year whether the seed germinates terrestrially or submerged. In nature the change from divided to entire leaves is seasonal but is rarely synchronous for all branches of a single plant and usually there are some branches that throughout the season never produce entire leaves. The first flower usually develops about two internodes before the first entire leaf is formed. Entire leaves are always associated with flowers but flowers may develop on stems bearing only divided leaves. The life history of *R. aquatilis* is occasionally completed without any entire leaves being produced.

The apex that produces entire leaves must be under water and if it is raised above the water surface divided leaves of the terrestrial kind develop (see page 70). The depth of the apex below the surface of the water is not very critical and entire leaves have been produced as much as 1 m deep in clear water. Very deep shade will inhibit the production of entire leaves but it also adversely affects the general growth and inhibits flowering. To investigate the effects of water as a selective filter of light

plants were cultivated terrestrially under glass tanks containing water but no change in leaf-form was seen. Glass alone above aquatically cultivated plants does not inhibit the production of entire leaves.

Temperature alone seems unimportant as plants cultivated in greenhouses under different temperature regimes changed from divided to entire leaves at approximately the same time as plants cultivated outdoors.

These observations led to experimental work on photoperiodic responses. Even-aged ramets of *R. aquatilis* (A-6) were cultivated submerged in winter at constant temperatures of 10°C and 18°C. Mercury vapour lamps producing 6.5 gm cal/dm²/min at the water surface with a rhythm of 16 hrs. light and 8 hrs. dark initiated the production of flowers and entire leaves in 10 days at 18°C and 14 days at 10°C. The controls under normal winter light remained in the divided-leaved state without flowering. When the plants subjected to the 16 hr photoperiod were returned to normal winter daylight the shoots bearing entire leaves gradually died, growth being resumed by branching from the divided-leaved portion of the shoot. It appears that subject to the apex being submerged the initiation of the entire leaves is under photoperiodic control and is not correlated with age and is thus not a heteroblastic type of heterophylly in the sense of GOEBEL (1897). Experiments with different partial pressure of oxygen and carbon dioxide have not yet been attempted.

R. baudotii, *R. peltatus* and *R. penicillatus*

These species show responses essentially similar to *R. aquatilis*. They have divided first seedling leaves and entire leaves confined to the air-water interface; with submerged buds. *R. baudotii* and *R. peltatus* each have different strains with different photoperiodic requirements; the Mediterranean strains switch to entire leaves at shorter photoperiods than the Northern European ones. *R. peltatus* very rarely flowers without entire leaves. *R. penicillatus* is a large plant found in flowing water and is difficult to cultivate in small tanks. It is interesting to note that small cuttings of this species will not flower or develop entire leaves under artificial light although large plants cultivated outdoors behave in a similar manner to *R. aquatilis*. It is possible that there is some form of heteroblastic development in this species. Interspecific hybrids involv-

ing heterophyllous parent species invariably show instability in leaf-form.

R. tripartitus

The first seedling leaf of *R. tripartitus* is always entire at any time of the year whether the seed is germinated terrestrially or submerged. In long or short photoperiods the leaves remain entire if the plant is kept warm (10°C or more). Once three or more entire leaves have developed I have been unable to induce the production of divided leaves. Divided leaves have only been induced in cultivation by placing germinating seeds in water between 4°C and 6°C under short photoperiods (12 hrs or less).

In nature at The Lizard, Cornwall, England, *R. tripartitus* when submerged, develops divided leaves up to the middle of March and by the beginning of April when there are approximately 12 hrs of light and 12 hrs dark the shoots develop entire leaves. During early April 1957, 1958 and 1963 when these observations were made, the water temperature at The Lizard varied between 11°C and 16°C . *R. tripartitus* frequently over-winters as a terrestrial plant in an entire-leaved state and is often found at the edge of pools containing the species in a divided-leaved state. In *R. tripartitus* there appears to be no correlation between heterophylly and heteroblastic development.

R. lobbii

I have not succeeded in cultivating *R. lobbii* but personal communications with LYMAN BENSON (Pomona) and STANTON COOK (Oregon) suggest that its heterophylly reaction is similar to *R. tripartitus*. Morphologically these two species are very similar, differing only in floral features.

R. ololeucos

This species occupies a position with regard to heterophylly somewhat intermediate between *R. aquatilis* and *R. tripartitus*. The first seedling leaf is more or less intermediate between being divided and entire. When germinated in cold or warm conditions, terrestrially or submerged and subjected to long photoperiods the first seedling leaf is entire but deeply-lobed, while in short photoperiods it is divided. Entire leaves develop only during long photoperiods but unlike *R. aquatilis* they may de-

velop from emergent buds. A unique feature of *R. ololeucos* is that when an entire-leaved shoot is put in short photoperiods it reverts to divided leaves whether it is cultivated terrestrially or submerged. Flowers may be borne on divided- or entire-leaved shoots.

R. saniculifolius

This species is an obligate annual and shows true heteroblastic development in the sense of GOEBEL (1897) with an irreversible heterophylly sequence that is barely influenced by the external environment. The first seedling leaf is linear. When *R. saniculifolius* is cultivated in a submerged or terrestrial environment, under long or short photoperiods, it develops three to six divided leaves before switching to entire leaves. Flowering starts with the production of the first entire leaf. Only if the seedling is put under conditions of stress such as deep shade or low temperature can the divided-leaved stage be prolonged, but under these conditions the plant remains sterile and shows a considerable loss of vigour.

The Stipules

The presence of stipules in the *Ranunculaceae* has not been generally recognized. EICHLER (1861) and COOK (1963) have discussed the morphology of stipules in *Thalictrum*, *Trollius*, *Caltha* and some species of *Ranunculus*. The stipules of *Batrachium* show proleptic growth, that is, they anticipate the growth of the leaf proper. While in bud the stipules of all the species look very similar and on old shoots the stipules tend to become torn or detached. For comparative purposes it is therefore best to compare stipules of the first fully expanded leaf. For any particular plant the stipule shape remains very constant and is barely influenced by external environmental conditions. In heterophyllous species the stipules of entire and divided leaves are similar.

All species have characteristic stipule shapes (fig. 2) which can be useful characters when used in conjunction with other features. The overall shape of the stipule is occasionally difficult to determine and requires careful dissection but the degree of adnation to the petiole is easily seen and taxonomically useful.

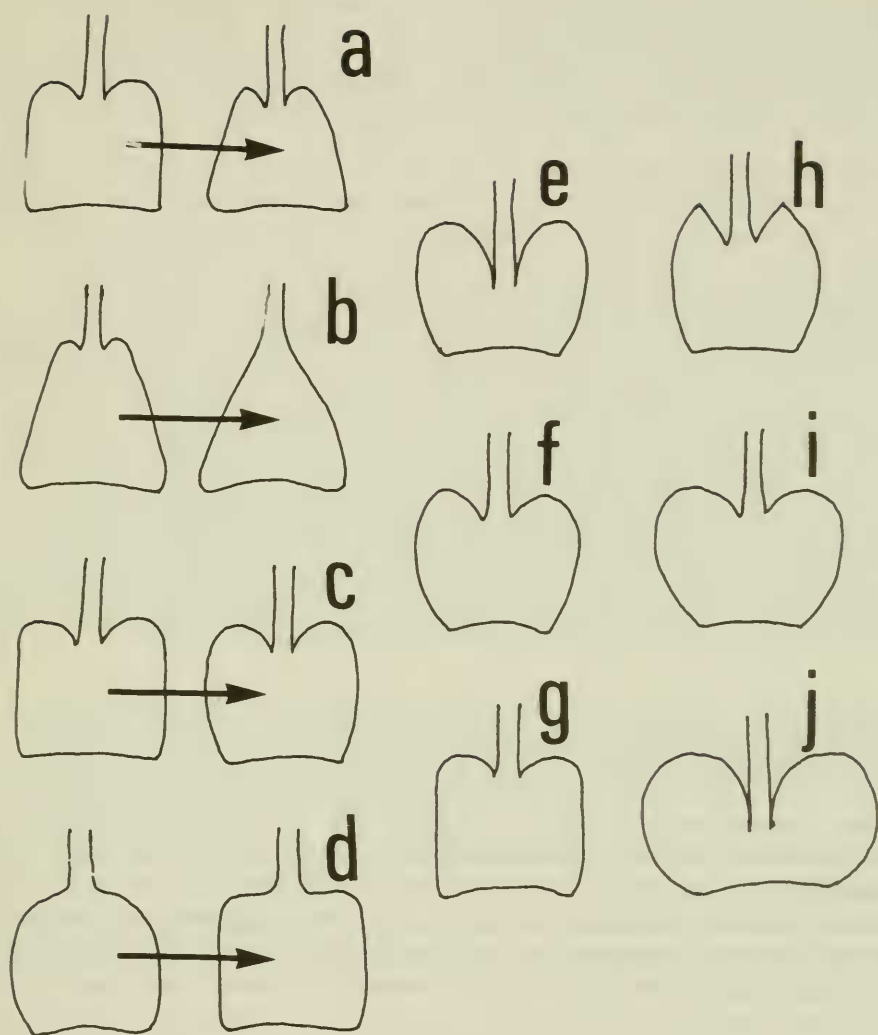


Fig. 2.: Stipule shapes: a) *R. peltatus*, *R. sphaerospermus*, *R. flavidus*; b) *R. aquatilis*; c) *R. trichophyllus*, *R. rionii*; d) *R. fluitans*; e) *R. omiophyllus*; f) *R. circinatus*, *R. longirostris*; g) *R. saniculifolius*; h) *R. hederaceus*; i) *R. tripartitus*, *R. lobbii*, *R. oroleucos*, *R. penicillatus*; j) *R. baudotii*.

The divided leaves

The divided leaves have basically the same developmental pattern in all species. Normally there are two trichotomies followed by subsequent dichotomies. The number of subsequent dichotomies is very much under environmental control except in *R. fluitans* which rarely develops more than two.

The divided leaves of *R. tripartitus* and perhaps *R. lobbii* develop only from shoots submerged in water; in all the other species the divided leaves may develop from shoots grown in submerged or terrestrial environments. Generally speaking, the submerged leaves are dark green, with long, fine segments and are circular in transverse-section with a large-celled epidermis containing many chloroplasts and a mesophyll that is more or less undifferentiated with few chloroplasts. The aerial or terrestrial leaves are light green with short, thick segments that are oval in transverse-section, the epidermis is small-celled with very few chloroplasts while the mesophyll contains many chloroplasts and shows a certain amount of differentiation with a marked palisade on the adaxial side. The morphological differences between terrestrial and submerged leaves are fully described and illustrated by ASKENASY (1870) and GESSNER (1940).

R. aquatilis, *R. baudotii*, *R. peltatus* and *R. penicillatus* develop the terrestrial kind of divided leaf only under a regime of long photoperiods. If any of the above or any completely divided-leaved species are cultivated as terrestrial plants in a saturated atmosphere the leaves have all the morphological characteristics of the submerged kind in short photoperiods and resemble the normal terrestrial kind in long photoperiods. Under a regime of long photoperiods in normal conditions the development of the terrestrial or submerged type of leaf is a direct plastic response dependent on the presence or absence of water. Under some abnormal conditions such as in a carbon dioxide-free air or under very low light intensity a terrestrially cultivated plant will resemble a submerged one. GESSNER (1940) has described the behaviour of *R. baudotii* under many abnormal conditions.

From a taxonomic point of view the morphology of the submerged divided leaves is of some value. *R. circinatus* is unique in that the leaf segments all lie in one plane. *R. fluitans* is easily recognized as it has an elongated obconical leaf

that is usually more than 8 cm long with thick, flaccid segments that are rarely more than four times forked. *R. tripartitus*, *R. lobbii* and *R. ololeucos* have segments that are very fine and hair-like. *R. baudotii* has characteristic yellowish-green leaves with rather long, almost setose ultimate segments. The divided leaves of the other species are virtually indistinguishable; in outline they are obconical to globose with fine, divergent, rigid or flaccid segments, the amount of branching is very variable and largely under environmental control. *R. trichophyllus*, for example, may have from 15 - 200 ultimate segments.

The presence of rigid or flaccid leaves has been frequently used in taxonomy of this group but it is a difficult character to use as it is easily modified by external environmental conditions and cannot be detected on herbarium specimens. *R. aquatilis* and *R. trichophyllus* have both rigid and flaccid leaved strains. If a rigid-leaved strain is grown in deep water (1 m or more), in low light intensity, in a constricted space (an aquarium tank) or in swiftly flowing water, the phenotype will have flaccid leaves. The flaccid-leaved strains have been induced to become rigid by cultivation in sea water, but in fresh water they often appear rigid when covered with epiphytic algae or encrusted with lime.

The length of the petiole is of limited taxonomic value as it is easily modified. Generally speaking, in winter or in summer on terrestrial plants the petiole is long, while in summer, if the plant is growing well, it is short.

The terrestrial divided leaves offer virtually no diagnostic features and are extremely similar between species. In all species they are long-petiolate and much branched, with rigid slightly flattened segments. They are also much smaller than the submerged leaves.

The entire leaves

The shape and size of the lamina of the entire leaf is somewhat plastic and is modified by external environmental conditions. On immature stems the overall outline of the leaf is reniform in all species. In *R. aquatilis*, *R. peltatus*, *R. omiophyllus* and to a lesser degree in *R. baudotii* the leaves become suborbicular or orbicular as the stem matures.

The depth of the sinus is a useful character but it can be

modified and leaves produced under water tend to have deeper sinuses. Occasionally on senescent stems the leaves have shallower sinuses.

The leaf lobes are cuneate in all species except *R. hederaceus*, which has lobes broadest at the base. The number of lobes is reasonably constant for each species. *R. hederaceus*, *R. ololeucos*, *R. lobbii*, *R. tripartitus* and *R. baudotii* have three lobes, *R. aquatilis*, *R. peltatus* and *R. penicillatus* have five lobes and *R. omiophyllus* and *R. saniculifolius* three or five lobes. The number of lobes varies slightly with maturity; when immature the number is low and when mature or senescent it is high. *R. peltatus*, for example, usually develops one or two three-lobed leaves at first, then five-lobed leaves for most of the season and finally a few seven-lobed leaves as it becomes senescent.

The margin of the leaf is usually crenate in all species except *R. aquatilis* which tends to have a dentate margin. The margin tends to be dentate in *R. tripartitus*, *R. baudotii* and *R. peltatus* if the leaves develop under water or in shade, however, plants grown under these conditions tend to look etiolated and have very long internodes and petioles.

The intermediate leaves

In the heterophyllous species of subgenus *Batrachium* the change from divided to entire leaves is usually abrupt but occasionally *R. baudotii*, *R. aquatilis*, *R. peltatus* and *R. penicillatus* develop a few leaves that are neither divided nor entire but a mixture of the two. Except for *R. baudotii* these intermediate leaves are usually borne on plants growing in poor conditions or plants showing high pollen sterility. They bear no resemblance to the sequential intermediate leaves of *R. flabellaris* and *R. gmelinii* of subgenus *Ranunculus*.

In subgenus *Batrachium* the form of these mixed intermediate leaves is characteristic for particular genotypes and is a valuable taxonomic character for indicating parentage of hybrids. Figure 3 shows some characteristic types of intermediate leaf. *R. peltatus* and *R. penicillatus* usually develop capillary segments distally from the entire portion of the leaf while *R. aquatilis* usually develops capillary segments at the proximal region with entire portions at the distal ends. In these three species the leaves are usually radially asymmetrical and it is not

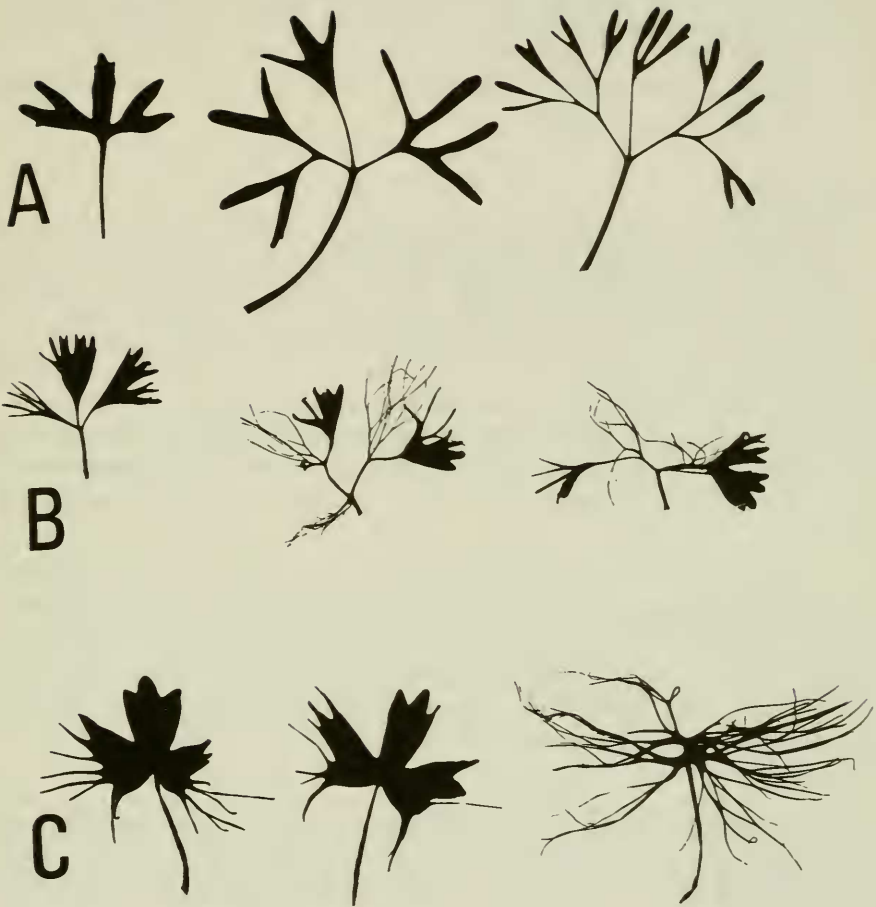


Fig. 3: Intermediate leaf-shapes: A) *R. baudotii*; B) *R. aquatilis*; C) *R. peltatus*.

unusual for some lobes to be divided and others entire.

R. baudotii develops intermediate leaves that are usually radially symmetrical with the proximal region divided and the distal region entire. This species is, however, more plastic in its heterophylly responses than other species and it is discussed in more detail on page 110.

The peduncle

The absolute length of the peduncle in fruit is characteristic for each species and is an important taxonomic feature, but it must be used with some caution. BUTCHER (1940) found that when mature plants were submerged in deep water some species responded by elongating their peduncles while others remained unchanged. My own experimental work indicates that within species there are frequently elongating and non-elongating strains. In the elongating strains it has been found that the peduncle and the petiole of the opposed entire leaf respond to the same degree so that the ratio of the lengths of those two organs remains constant. This taxonomic character is easily assessed and is given in each description. All plants when submerged in deep water usually respond by elongating their internodes. Internode length, however, is not correlated with peduncle length. Many other factors such as light intensity, competition, temperature, etc. influence internode length so it is not a reliable indicator of submergence.

BABINGTON (1855) and HIERN (1871) have used tapering and non-tapering peduncles as taxonomic characters. My own experience of this character is that it is inconsistent and of no value.

The flower

In order to find variation in size, shape and number of floral organs measurements were made on flowers collected from populations in nature and plants cultivated under different conditions. The range of variation was calculated and checked against herbarium material.

The following measurements were made on the flower: sepal length and maximum width, petal number, length, width and position of maximum width (to get some measurement of shape), number of veins at the base and distal end of each petal, nectary

shape, stamen number and length, carpel number and hairiness (three arbitrary units), and receptacle hairiness and shape. The relevant information thus gained is incorporated into each specific description.

The sepals

The sepals are blue or blue-tipped in *R. tripartitus*, *R. lobbii*, *R. ololeucos* and *R. longirostris*. In all other species they are green when young becoming brown at maturity. The presence of a blue pigment is a useful and reliable taxonomic character and is easily seen on even the oldest herbarium specimens. All hybrid plants to date involving a blue-sepalled parent have had blue sepals.

In all species the sepals are more or less caducous but in some species they become reflexed before falling off. Although this has been mentioned in specific descriptions, it is not a reliable character.

The petals

All species of *Batrachium* have non-glossy petals (PARKIN 1928) and all species have white petals with a yellow claw, except for *R. flavidus* which has yellow petals and *R. ololeucos* which may have entirely white ones.

All species show considerable variation in the number of petals. The usual number is five for all species except *R. fluitans* which is very variable and has a mean of about six. The petal shape is fairly constant and distinctive for all species. During anthesis some species have contiguous or over-lapping petals while the others have non-contiguous ones. This is an easily seen distinction between some otherwise rather similar species such as *R. trichophyllum* and *R. aquatilis*. After anthesis the petals tend to roll up along the lateral edges thus becoming non-contiguous but examination of the stamens will show whether anthesis is finished or not.

The length of the petal is characteristic for each species but is often modified by external environmental conditions. Petal length is, however, positively correlated with sepal length (fig. 6) and the ratio between the two is often more useful taxonomically.

The number of veins in the petal was used by HIERN (1871)

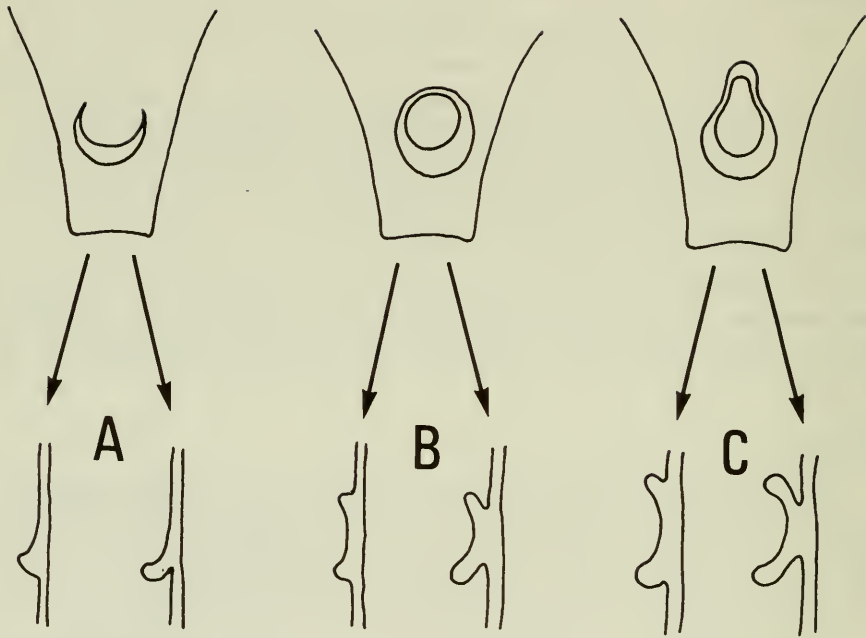


Fig. 4.: Nectar-pit types in surface view (above) and in lateral and median longitudinal sections. A) lunate; B) circular; C) pyriform.

but this character is of little use as it appears to be correlated with the vigour of the plant.

The nectar-pit is a very useful taxonomic character but must be used with reserve. Figure 4 shows the range of nectary types. The nectar-pit is elongated and more or less pyriform in *R. peltatus*, *R. penicillatus* and *R. fluitans*, circular in *R. aquatilis* and lunate in all the other species. The ontogenetic sequence to the pyriform type passes through lunate and circular phases so it is essential that only mature petals are examined. Another difficulty is that it is not always easy to distinguish nectary types on dried specimens so it is necessary to rehydrate a petal. ARBER (1936), BENSON (1940) and LEINFELLNER (1959) have examined the nectaries in *Ranunculus* and are agreed that the lunate type is very much reduced. PERCIVAL (1961) examined the sugars in the nectar of *R. baudotii*, *R. hederaceus* and *R. trichophyllus* and found the nectar to be dominated by sucrose.

The number of stamens and carpels

Stamen and carpel number have been used as taxonomic characters by nearly all workers on *Batrachium*. These characters are of value but can be easily modified by changes in environmental conditions. As the numbers of stamens and carpels give a semi-quantitative indication of a plant's vigour they have been studied in more detail so that they could be used in genecological work. Figure 5 shows the variation in stamen and carpel number and sepal and petal length in a population of *R. tripartitus* from Kynance, The Lizard, Cornwall, England. The dotted line represents the total range and the solid line represents the standard deviation. In all cases ten flowers were examined; this somewhat small sample size was dictated by the number of plants in the population. A, B and C were samples taken from the wild. B and C were collected on 23 March 1957 while A was collected on 29 March 1958. A and B were in a heterophyllous state and C in an entire-leaved state. The range and means of the stamen and carpel numbers of A, B and C are rather different and as no genetical differences have been detected, this difference is probably phenotypic. This is supported by examining D, E and F which are ramets of B cultivated in a cool greenhouse at Cambridge Botanic Gardens. D was heterophyllous, being cultivated in an aquarium tank, while E was entire-leaved, being cultivated terrestrially on water-logged soil. Both were sampled on

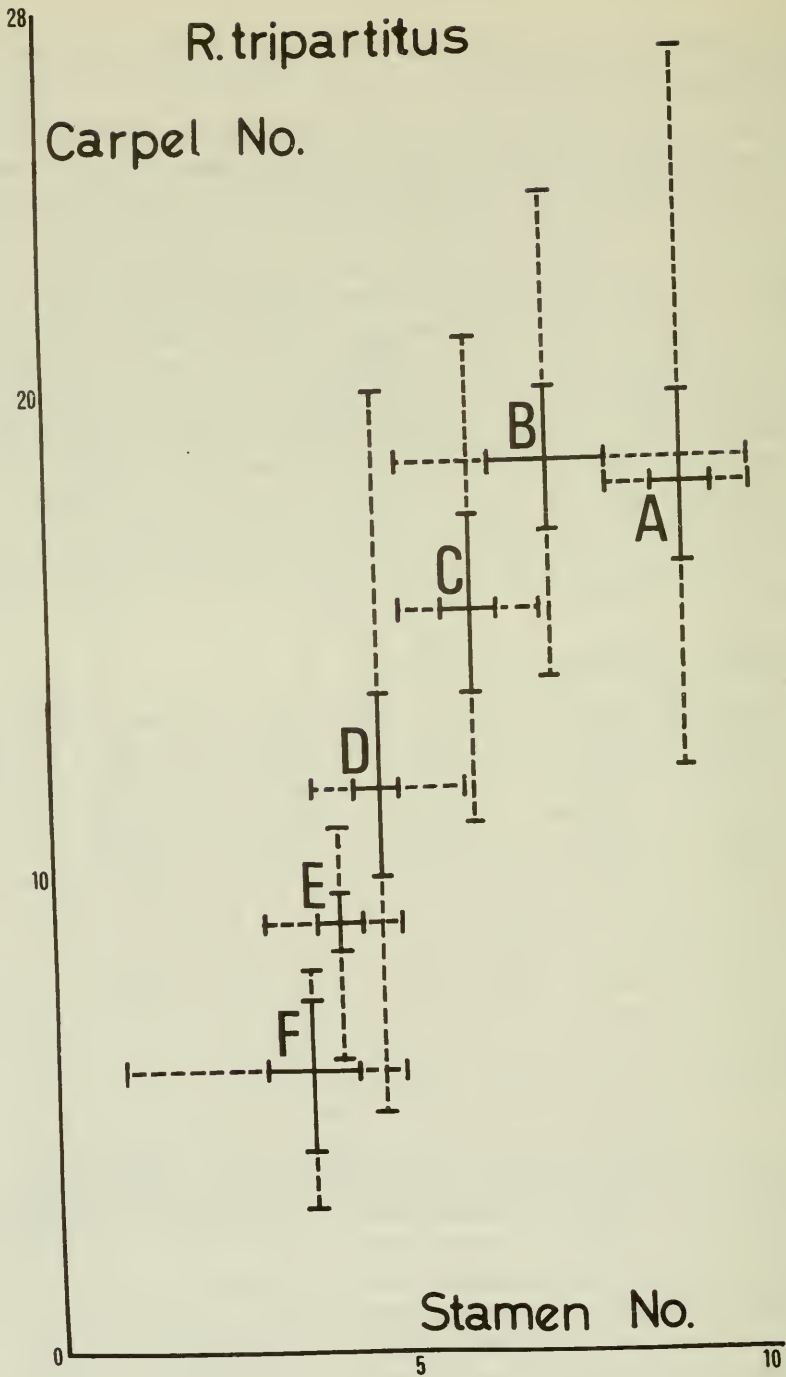


Fig. 5.: The variation in stamen number and carpel number in *R. tripartitus* (see text for explanation).

16 May 1957; F was the same plant as E but sampled on 26 February 1958.

To study the variation in the number of stamens and carpels in more detail, an experiment was carried out using different quantities of available nutrients. The plant chosen for this experiment was *R. penicillatus* var. *calcareus* from a chalk stream at Puddletown, Dorset, England. It was chosen as it has a very large number of carpels and stamens in the wild.

Equal-aged and equal-sized clonal cuttings were planted in equal-sized pots; three pairs were put in John Innes Number I potting compost. The first pair were put in 25 cm of gently flowing water in the artificial stream at Cambridge, the second pair in 25 cm of distilled water in glass tanks and the third pair grown terrestrially in saturated soil. Another three pairs of cuttings were potted in washed silver sand and put alongside the first three pairs. After twenty days the flowers from each pot were gathered and the petal and sepal lengths and stamen and carpel number determined. Unfortunately, the terrestrial plants did not flower and the plants in pots of silver sand in the stream became uprooted and were lost.

Figure 6 is a pictorialised scatter diagram showing the relationship between the carpel and stamen numbers and sepal and petal lengths. It can be seen that petal length and sepal length are positively correlated and that the lengths decrease with poorer conditions. The interesting thing is that the carpel number tends to decrease first and at a faster rate than the stamen number. The stamen number only decreases rapidly when the plants are under conditions of stress; in this case, rooted in washed silver sand and grown in distilled water.

This experiment indicates that the stamens are better equipped to compete with carpels when the quantity of available nutrients are limited. Stamen number is more stable and is, perhaps, a more reliable taxonomic character, while carpel number responds to slight environmental differences and is a better measurement of small scale ecological pressures. Measurements on other species support this statement. Taking SALISBURY'S (1934) data on *R. hederaceus* collected from 190 flowers from two wild populations (one in Devon and one in Surrey) the anther number had a mean of 7.6, standard deviation of 1.4 and a range of 4 - 11, while from two different populations (one in

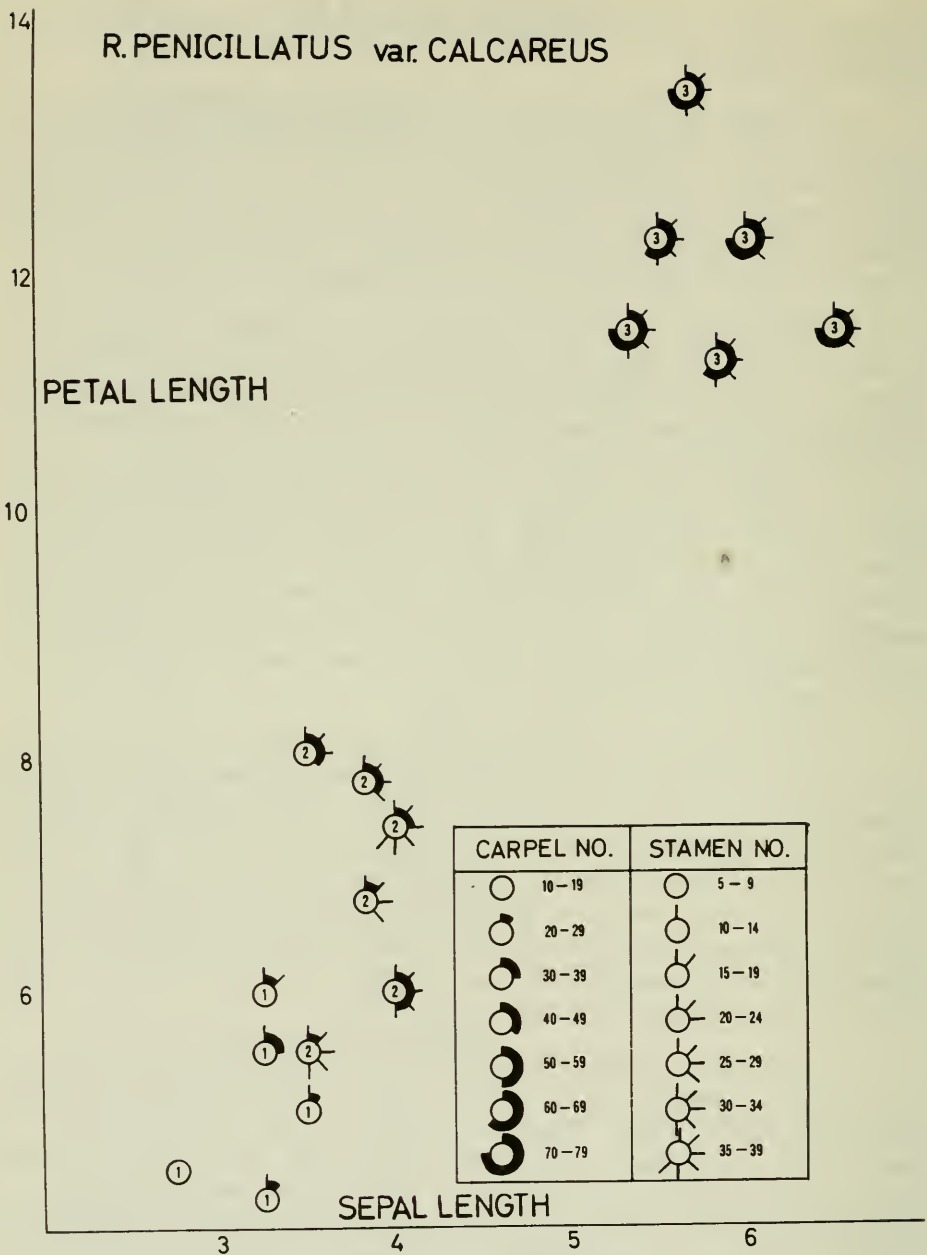


Fig. 6.: A pictorialised scatter diagram illustrating the relationships between carpel and stamen numbers and sepal and petal lengths. (3 = stream culture, normal potting mixture; 2 = tank culture, normal potting mixture; 1 = tank culture, potted in washed silver sand).

Cornwall and one in Kent) I found a mean of 7.6, standard deviation of 1.7 and a range of 5 - 11 from 20 flowers. The carpel number from SALISBURY had a mean 19.5, standard deviation 5.5 and range 9 - 32 on 400 flowers, while I had a mean 23.3, standard deviation 2.4 and a range 12 - 42 from 20 measurements.

R. lobbii is the only species that can be determined on carpel number, as it is unique in having a very low and constant number; the total range recorded is 2 - 6.

The stamen

No constant specific morphological characters have been found. FREYN (1881) used the shape of the anther and the relative length of stamens and carpels as important diagnostic characters. I find that the anther continues growth until dehiscence and that the filament elongates until abscission so that FREYN'S characters are merely ontogenetic stages in the development of the stamen.

The achene

The morphology of the achene provides the most important character for separating the subgenus *Batrachium* from the rest of *Ranunculus* and is described in detail by COOK (1963). The overall shape is of little value as all species have globose to broadly obovoid achenes that are slightly compressed laterally and have weak dorsal and ventral ridges. *R. baudotii* is unique in that it has winged dorsal and ventral ridges; they are best seen on dried achenes. The length of the achene has been used by BENSON (1948) but I find it of limited use as it depends on how many achenes develop and their position on the receptacle. In a vigorous plant when pollination is poor the few achenes that develop are larger than the many achenes that develop when pollination is good. The achenes at the top of the receptacle are longer than those at the base. In spite of these variations there is a discontinuity in length; *R. rionii*, *R. sphaerospermus* and, perhaps, *R. flavidus* have achenes less than 1 mm long, all other species have achenes 1.25 - 2.5 mm long.

Achene hairiness is a very useful character for some species but must be used with caution for others. *R. hederaceus*, *R. omiophyllus*, *R. tripartitus*, *R. lobbii*, *R. olroleucos* and *R. baudotii* are invariably glabrous, *R.*

rionii, *R. sphaerospermus*, *R. longirostris* and *R. saniculifolius* are glabrous or hairy; the other species are hairy when immature, often very sparsely so, but may be glabrous at maturity.

The style

After maturity of the embryo sac the style elongates until pollinated. When pollination is withheld, the style frequently reaches a length of 1.5 mm. The species investigated are largely self-pollinated and the style rarely exceeds 1 mm. According to BENSON (1948) and MASON (1957) the styles of the endemic American species *R. lobbii* and *R. longirostris* are consistently about 1.5 mm long. The style is caducous in all species except *R. longirostris* where it is largely persistent and forms a beak 0.7 - 1.1 mm long on the ripe achene.

The position of the style on the achene is a useful character. In *R. omiophyllus* and *R. longirostris* it is terminal, in *R. fluitans* and *R. circinatus* it is consistently lateral, and in the other species it is lateral to subterminal, the achenes at the base of the receptacle usually have a lateral style while those at the top are subterminal.

The receptacle

The receptacle elongates in fruit in *R. saniculifolius*, *R. baudotii*, *R. rionii*, *R. sphaerospermus* and, perhaps, *R. flavidus*. In all other species it remains more or less globose.

Hairiness of the receptacle is a very reliable and useful character as it is either densely hairy or glabrous, except in *R. fluitans* which is usually glabrous but occasionally sparsely hairy. In all crosses between parents with hairy and glabrous receptacles, the first generation hybrids have had hairy receptacles.

Taxonomic Treatment

No satisfactory classification of the genus *Ranunculus* as a whole, even at subgeneric or sectional level, exists. The shortcomings of the existing classifications are pointed out by DAVIS (1960). The status of *Batrachium* has varied from

section to genus. It is felt that *Batrachium* hardly deserves generic rank as it cannot be separated from *Ranunculus* on any single character as pointed out by COOK (1963). The choice of rank appears to lie between that of section or subgenus. It is felt that the level of differentiation is sufficient to merit subgeneric rank and, as this category has been frequently adopted, I prefer to retain *Batrachium* as a subgenus of *Ranunculus*.

Ranunculus subgenus *Batrachium* (DC.) A. Gray, Proc. Am. Acad. 21: 363 (1886).

Batrachium as a section of *Ranunculus* has the following citation: DC., Syst. 1: 232 - 233 (1818) and as a genus: S. F. Gray, Nat. Arr. Brit. Pl. 2: 720 (1821).

Description

Aquatic or semi-terrestrial annuals or perennials. Leaves mostly cauline, entire or divided into capillary segments; stipules membranous, partly adnate to the petiole. Sepals usually 5, not petaloid, caducous. Petals 5 or more, non-glossy, white, with or without yellow claw or entirely yellow; nectar-pit lunate, circular or pyriform. Achenes not strongly compressed, with regular transverse ridges up to 1 mm apart on the lateral walls.

The type of *Batrachium* is *R. hederaceus*.

Key

1a Petals yellow (Himalaya Mountains):. . . 11. *flavidus*

1b Petals white, with or without yellow claw

2a Entire leaves present; divided leaves present or absent

3a Divided leaves absent

4a Immature achenes pubescent (sometimes sparsely and minutely so):. 7. *saniculifolius*

4b Immature achenes glabrous

5a Receptacle glabrous

6a Leaf segments broadest at sinus; petals not or scarcely longer than sepals:. . . 1. *hederaceus*

6b Leaf segments narrowest at sinus; petals 2 - 3 times
as long as sepals

7a Achenes 15 - 67; style terminal; leaves 3- or 5-lobed:
2. omiophyllus

7b Achenes 2 - 6; style lateral to subterminal; leaves
deeply tripartite: 4. lobbii

5b Receptacle pubescent

8a Petals more than 5 mm long; achenes winged; re-
ceptacle elongate in fruit: . . . 6. baudotii

8b Petals less than 5 mm long; achenes not winged;
receptacle not elongate in fruit:
3. tripartitus

3b Divided leaves present

9a Receptacle glabrous; achenes 2 - 6:
4. lobbii

9b Receptacle pubescent; achenes more than 6

10a Petals less than 5 mm long, narrowly obovate:
3. tripartitus

10b Petals more than 5 mm long, broadly obovate

11a Immature achenes glabrous

12a Receptacle elongate in fruit; mature
achenes winged; submerged divided
leaves robust, rigid (brackish water):
6. baudotii

12b Receptacle not elongate in fruit; mature
achenes unwinged; submerged divided
leaves very fine, flaccid (freshwater):
5. ololeucos

11b Immature achenes pubescent (sometimes
sparsely so)

13a Peduncle in fruit shorter than the
petiole of the opposed entire leaf;
nectar-pits circular; leaf-margin
dentate: . . . 10. aquaticus

- 13b Peduncle in fruit longer than the petiole of the
opposed entire leaf; nectar-pits lunate or pyriform;
leaf-margin crenate
- 14a Nectar-pits lunate; petals rarely exceeding 10 mm
long; receptacle elongate in fruit:
7. saniculifolius
- 14b Nectar-pits pyriform; petals usually exceeding
10 mm long
- 15a Mature divided leaves shorter than internodes;
leaf segments divergent: 8. peltatus
- 15b Mature divided leaves as long as or longer than
internodes; leaf segments subparallel:
17. penicillatus var.
penicillatus
- 2b Entire leaves absent
 - 16a Style persistent, at least $\frac{1}{3}$ as long as
achene: 15. longirostris
 - 16b Style not persistent or style persistent and
less than $\frac{1}{3}$ as long as achene
 - 17a Leaf segments lying in one plane;
14. circinatus
 - 17b Leaf segments lying in more than one
plane
 - 18a Mature achenes winged; sepals
usually blue-tipped:
6. baudotii
 - 18b Mature achenes not winged; sepals
never blue-tipped
 - 19a Petals rarely exceeding 5 mm long,
not contiguous during anthesis;
nectar-pits lunate
 - 20a Mature achenes less than 1 mm
long, subglobose, numerous
(60 - 90): 13. rionii

- 20b Mature achenes more than 1.5 mm long, ovoid to obovoid, few (rarely exceeding 35)
 - 21a Plant robust, erect, rooting only at lower nodes (not arctic-alpine):
 - 12. trichophyllus
subsp. trichophyllus
 - 21b Plant delicate, procumbent, rooting at most nodes (arctic-alpine):
 - 12a. trichophyllus
subsp. lutulentus
- 19b Petals exceeding 5 mm long, contiguous during anthesis, nectar-pits circular or pyriform
 - 22a Mature achenes less than 1 mm long, subglobose:
 - 9. sphaerospermus
 - 22b Mature achenes more than 1 mm long, ovoid to obovoid
 - 23a Mature divided leaves as long as or longer than internodes; leaf segments subparallel
 - 24a Receptacle densely pubescent:
 - 17a. penicillatus
var. calcareus
 - 24b Receptacle sparsely pubescent or glabrous:
 - 16. fluitans
 - 23b Mature divided leaves shorter than internodes; leaf segments divergent
 - 25a Ultimate leaf segments 200 or more:
 - 17b. penicillatus
var. vertumnus
 - 25b Ultimate leaf segments less than 100
 - 26a Nectar-pits circular; peduncle in fruit rarely exceeding 50 mm long:
 - 10. aquatilis
 - 26b Nectar-pits pyriform; peduncle in fruit usually exceeding 50 mm long:
 - 8. peltatus

Species non satis notae

R. bungei Steudel, Nomencl. Bot. 2: 433 (1841).

[R. hydrophilus Bunge. Enum. Pl. Chin. 2(1831) non Gaudich ex Mirb. Ann. Sci. Nat. sér. 1, 5: 105 (1825)]

I am not certain that this species belongs in subgenus *Batrachium* as I have not seen adequate material. The leaves are flabellate-cuneate in outline with subparallel oblong lobes. I have only seen material collected near Peking in China.

R. pueblensis W. B. Drew, *Rhodora* 38: 46 (1936).

This species differs from *R. trichophyllum* only in possessing slightly larger achenes (2.3 - 3 mm long) with stout recurved style bases. It is only known from Puebla, Mexico.

R. yesoensis Nakai, Bot. Mag. Tokyo 44: 523 (1930).

This species is known only from Japan and differs from *R. rionii* in possessing a glabrous receptacle. I have not seen any material of this species.

1. Ranunculus hederaceus L., Sp. Pl. 556 (1753).

R. hederaceus Salisb., Prod. Stirp. 373 (1796), nom. invalid.

Batrachium hederaceum (L.) S. F. Gray, Nat. Arr. Brit. Pl. 2: 721 (1821), nom. legit.

R. hydrocharis B. homiophyllum var. *hederaceus* (L.) Spenner, Fl. Frib. 3: 1008 (1829), nom. invalid.

R. hydrocharis Spenner "form"*) *hederaceus* (Salisb.) Hiern, J. Bot. Lond. 9: 67 (1871), nom. invalid.

*) HIERN'S "forms" or "ultimate forms" as he calls them on p. 44 loc. cit. have no definite taxonomic rank.

R. asarifolius Diard, in schaed. fide Rouy & Fouc.,
Fl. Fr. 1: 60 (1893).

Icones

Cosson, E. & Germain, E. Atlas Fl. Env. Paris pl. 1, fig. 1, 2
(1845).

Glück, H., Wasser- und Sumpfgewächse 4: t. 5, fig. 11 - 15, t. 6,
fig. 1 - 2 (1924).

Ross-Craig, S., Drawings of British Plants 1: 22 (1948).

Typification

BENSON (1954) designated the specimen on sheet number 74 (SAVAGE 1945) in the Linnaean Herbarium, Linnean Society, London (LINN) the lectotype of *R. hederaceus*. I have examined this specimen and can find no reason to doubt BENSON'S designation.

Description

Prostrate annual or perennial. Leaves entire, opposite or alternate; stipules ovate, adnate to petiole for more than 1/2 their length, apex acute; petiole 2 - 4 times as long as lamina; lamina 4 - 25 mm long, 3 - 35 mm wide, reniform to subcordate with 3, 5 or rarely 7 lobes; lobes broadest at base; margin entire or crenulate. Peduncles in fruit more or less equal to petioles of opposed leaves. Sepals (1.0) 2 - 2.5 (3.0) mm long, spreading. Petals (1.25) 2.5 - 3.5 (4.25) mm long, ovate, not contiguous; nectar-pits lunate. Stamens (4) 7 - 10 (11). Carpels (9) 18 - 24 (42), glabrous; style lateral to subterminal. Receptacle glabrous.

Distribution

R. hederaceus occurs in Europe and North America. In Europe (fig. 7a) it shows an Atlantic distribution but is widespread in inland districts of Britain. In North America (fig. 7b) it is confined to Newfoundland and the Chesapeake Bay region. It has been recorded from Dalmatia, Italy, Sicily, Iceland, Greenland and North West America (SALISBURY 1934) but I have not been able to trace herbarium material to support these records. It is likely that the Italian and Sicilian records are due to misidentifications of *R. omiophyllus* and the northern records misidentifications of *R. cymbalaria* Pursh. or *R. hyper-*



Fig. 7.: Distribution of *R. hederaceus*. a) Europe, b) North America

boreus Rottb.

The status of *R. hederaceus* in North America is problematical. It was first recorded by BOSC (BOSC & BAURILLARD 1821) from Carolina. GRAY (1886), FERNALD (1911, 1929 and 1931), DREW (1936) and BENSON (1948) considered it to be native while MACOUN (1891) and MORRIS (1900) regarded it as introduced. MORRIS wrote: "patches ... (Patuxent River) badly cut up by the passage of teams over a temporary farm road", while FERNALD wrote: "apparently indigenous in Newfoundland especially since it shares natural and undisturbed habitats with or near other European types". In Europe it is usually found in disturbed habitats. There seems little doubt that it was introduced in Carolina. WALKER did not record it in 1788 in *Flora Caroliniana*; it was recorded by BOSC in 1821 and reported extinct by ELLIOT in 1824. The general distribution in North America would suggest that it was introduced when compared with other examples quoted by LINDROTH (1957). There are, however, two species of fern, *Schizaea pusilla* Pursh and *Woodwardia areolata* (L.) Moore which share almost the same distribution in North America and which are certainly not European introductions.

FAEGRI (1960) considered *R. hederaceus* to have been introduced in Norway where it is confined to a small coastal area near Trondheim.

Ecology & variation

Combined with *R. omiophyllus*, see page 93.

2. Ranunculus omiophyllus Ten., Fl. Nap. 4: 338 (1830).

R. coenosus Guss., Suppl. Fl. Sic. Prodr. 187 (1832).

? *R. aquatilis* L. var. *homophyllus* (Ten.) Moris, Fl. Sard.
1: 26 (1837).

R. lenormandii F. Schultz, Bot. Zeit. 20: 726 (1837).

R. reniforme Desportes, Fl. Sarthe & Mayenne 3 (1838).

R. hederaceus L. var. *grandiflorus* Bab., Man. Brit. Bot.
5 (1843).

Batrachium lenormandii (F. Schultz) F. Schultz, Arch.
Fl. Fr. & Allem. 70 (1844).

B. coenosum (Guss.) Nyman, Bot. Notiser 100 (1852).

R. hydrocharis Spenner, "form" *homoeophyllus* (Ten.),
"form" *lenormandii* (F. Schultz) Hiern, J. Bot.
Lond. 9: 66 (1871), nom. invalid.

R. mauritanicus Pomel, Nouv. Mat. Fl. Atl. 249 (1874).

R. hederaceus L. subsp. *coenosus* (Guss.) Nyman, Consp.
Fl. Eur. 1: 16 (1878).

R. hederaceus L. var. *coenosus* (Guss.) Cosson, Comp.
Fl. Atl. 2: 15 (1887).

R. hederaceus L. proles *homoeophyllus* (Ten.) Rouy &
Fouc., Fl. Fr. 1: 60 (1893).

R. hederaceus L. var. *homoeophyllus* (Ten.) Fiori &
Paoletti, Fl. Anal. Ital. 1: 500 (1898).

B. omiophyllum (Ten.) C. D. K. Cook, Mitt. Bot. München
3: 600 (1960). nom. legit.

Icones

Cosson, E. & Germain, E. Atlas Fl. Env. Paris pl. 1, fig. 3, 4
(1845).

Glück, H. Wasser- und Sumpfgewächse 4: t. 5, fig. 4 - 6 (1924).

Ross-Craig, S. Drawings of British Plants. 1: 21 (1948).

Typification

Written below TENORE'S original description (op. cit. p. 339) appears "Nasce ne' fossi fangosi della Basilicata e della Calabria: a Balvano, Cassano, Corigliano". In TENORE'S own herbarium at Naples (NAP) the most complete specimen is one collected from Balvano; it is adfixed to a label bearing *R. omiophyllus* in TENORE'S own handwriting and I designate this specimen the lectotype of *R. omiophyllus*.

The spelling of *R. omiophyllus* is TENORE'S own and appears in his handwritten and printed works.

Description

Prostrate annual or perennial. Leaves entire, opposite or alternate; stipules ovate, adnate to petiole for $1/2$ or less their length, apex obtuse; petiole 3 - 6 times as long as lamina; lamina 2 - 26 mm long, 3 - 32 mm wide, reniform to suborbicular with 3, 5 or rarely 7 lobes; lobes narrowest at base; margin crenate. Peduncles in fruit equal to or less than petioles of opposed leaves. Sepals (1.75) 2.5 - 3 (3.75) mm long, reflexed. Petals (3.75) 5 - 6 (7.00) mm long, ovate, not contiguous; nectar-pits lunate. Stamens (5) 7 - 10 (13). Carpels (15) 20 - 50 (67), glabrous; style terminal. Receptacle glabrous.

Distribution

R. omiophyllus is confined to Europe and North Africa (fig. 8). In Europe it shows a distinct Atlantic distribution from North France to Portugal but is also present in mountainous districts in South Italy and Sicily. In Britain the limits of distribution follow extremely closely the August 3 inch isohyetal. In North Africa it is confined to the coastal mountains of Algeria. According to MOGGI (1963) most species common to Atlantic Europe and South Italy migrated along the Appenine Mountains and are not found in North Africa. *Genista anglica* L. and *R. omiophyllus* are, perhaps, the only two Atlantic-South Italian species that are absent from the Appenines but present in North Africa.

MORIS (1837) described a plant called *R. aquatilis*



Fig. 8.: Distribution of *R. omiophyllus*.

var *homophyllus* (Ten.) from Sardinia. The description is inadequate and as I have seen no herbarium specimens some doubt about this record must remain.

Ecology

R. hederaceus and *R. omiophyllus* are found on wet mud, in small streams, ditches and ponds, often in temporary water and usually in somewhat open and disturbed habitats.

SALISBURY (1934) reported both species to be winter annuals but this appears to be an over-simplification. If cultivated in waterlogged soil and not subjected to interspecific competition, they behave as perennials and survive for at least six years. In winter, both species form small tight cushions which are very resistant to desiccation, freezing and shade, but in summer they develop a spreading habit and are very susceptible to desiccation and shade. When cultivated in mud with *Peplis portula* L., both species behave as winter annuals. Seed germination is very irregular when the achenes are kept wet but if the achenes are dried and then rewetted, nearly complete germination takes place. Both species, in nature, may behave as spring or winter annuals or as perennials depending on the local water regime and competing species.

In cultivation, British material of each species grows well on calcareous and non-calcareous soils and no interspecific differences in vigour have been detected. Similarly Sicilian and British material of *R. omiophyllus* do not show any differences in vigour when cultivated side by side under different conditions.

Putative records of *R. omiophyllus* and *R. hederaceus* from inter- and post-glacial times are recorded by GODWIN (1956) but after re-examination of some fossil material I find it impossible to distinguish these species from their quaternary remains so, unfortunately, no acceptable information can be reported about their geographical ranges in the past.

The flowering times of *R. hederaceus* and *R. omiophyllus* show a considerable range of variation. When cultivated in cool but frost-free greenhouses at Cambridge, München and Liverpool University Botanic Gardens, occasional flowers were formed throughout the year but most flowers were produced between February and November. Both species are fairly sensitive to constant high temperature and if cultivated in a greenhouse

with a continuous temperature of 21°C or more they soon die. In nature *R. hederaceus* has been seen in flower and fruit in March 1958 in South Cornwall, England, while in South East Scotland in the same year flowering was just starting in May. In Norway and in the higher parts of the Sierra Nevada in Spain flowering begins as late as August. *R. omiophyllus* is equally variable and plants have been seen in flower in North Wales in November and February, in the Madonie Mountains of Sicily flowering commences during April. In cultivation flowering does not cease abruptly at any particular time of the year. In nature, however, flowering in each species is usually stopped by the plants being smothered by later-growing species such as *R. scleratus* L., *Peplis portula* L. and *Montia fontana* L. or by the habitat drying out or freezing.

Pollination and fertilization have been described by COOK (1963) - see also page 183. After fertilization the pedicel bends downwards forcing the developing fruits into the substratum. The achenes are probably dispersed in mud, carried by animals or machines or occasionally, they are liberated in water and then they may be dispersed by water currents or by surface contact with larger animals.

R. hederaceus and *R. omiophyllus* are largely sympatric, morphologically very alike, and share a similar ecological niche, occasionally being found growing together. SALISBURY (1934) reported that *R. omiophyllus* was invariably associated with peaty waters while *R. hederaceus* was more tolerant of waters well supplied with mineral salts, but he had, however, seen both species growing intermingled. In Britain, his generalization may be correct but in the Madonie Mountains of Sicily *R. omiophyllus* was found growing in eutrophic conditions around cattle troughs on calcareous substrata, the kind of conditions, in fact, where one expects to find *R. hederaceus* in Britain. It may be that where these two species are not competing they exhibit wider ecological amplitudes.

Variation

The plants that have been maintained in cultivation are listed on page 55. Crosses between H-2 and H-4, and H-2 and H-5 have been made (see page 187) and batches of 25 seedlings from selfed hybrids H-2 X H-4 and H-2 X H-5 have been raised. All these cultivated plants have been compared and no genotypic

variation has been detected. No suggestion of possible genotypic variation has been seen from the examined herbarium material.

Under *R. hederaceus*, GLÜCK (1924, 1936) recognised one variety, *R. hederaceus* var. *coenosus* (Gussone) Cosson which is referable to *R. omiophyllus*. Under *R. hederaceus sensu stricto* GLÜCK recognised and described six formae (*natans*, *amphibius*, *latifolius*, *terrestris*, *pumilus* and *reniformis*). Under *R. omiophyllus* (*R. lenormandii*) he recognised and described three formae (*natans*, *amphibius* and *terrestris*). To a great extent GLÜCK based his formae on more or less arbitrarily chosen size categories. My cultivation experiments suggest that these formae are no more than phenotypic modifications as plants matching the descriptions of each of GLÜCK'S formae have been induced from ramets of single clones of each species. GLÜCK'S descriptions, tables and illustrations (GLÜCK(1924) 4: 580-591, t. 5, 6) give a very good indication of the plasticity of these species.

The plastic variation pattern in both species is very similar and may be due to homologous variation indicating a close patristic relationship. However, the behaviour of both species is not always predictable and, for example, merely cultivating plants terrestrially does not necessarily cause them to resemble forma *terrestris*. Each phenotype results from the interaction of many environmental factors and is constantly changing. The water regime is very important but so are light intensity, photoperiod, competition, temperature, substrate conditions, age of plant, etc.

Leaf shape and size are particularly plastic. In *R. hederaceus*, for example, a terrestrially cultivated plant in summer will usually be compact with leaves 4 - 8 mm long and 3 - 10 mm wide, while a plant of the same age at the same time cultivated in 5 cm of water will be spreading and normally have leaves 17 - 25 mm long and 25 - 35 mm wide. When a plant is growing quickly in favourable conditions the leaves are usually 3-lobed with the lobes widest at the base but if the plant is grown in less suitable conditions, such as in deep water, shade or dry soil, the leaves become distinctly 5-lobed and the sinus may become deeper making the base of the lobe narrower, or the sinus may disappear, producing a typically reniform leaf. It is interesting to note that the synthesized autotetraploid (see page 176) nearly always has five lobes with a very much reduced sinus.

In spite of the extreme phenotypic plasticity in size and

leaf-shape the recognition of these species is not difficult since highly modified leaf-shapes are only manifest on mature or over-mature leaves while the immature leaves always show the characteristic form of each species.

3. Ranunculus tripartitus DC., Icon. Pl. Gall. Rar. 1: 15, t. 49 (1808).

Batrachium tripartitum (DC.) S. F. Gray, Nat. Arr. Brit. Pl. 721 (1821), nom. legit.

B. obtusiflorum sensu S. F. Gray, loc. cit.

R. aquatilis L. *A. heterophyllus* var. *lejospermus*, var. *micranthus* Wallroth, Sched. Crit. 285 (1822).

R. hydrocharis A. *heterophyllus* var. *tripartitus* (DC.) Spenner, Fl. Frib. 3: 1008 (1829), nom. invalid.

R. petiveri Koch in Sturm, Deutschl. Fl. 82, t. 2 (1840), pro parte.

R. petiveri Koch var. *minor* Koch, Syn. Fl. Germ. ed. 2, 13 (1843).

B. intermedium sensu Nyman, Syll. Fl. Eur. 175 (1854), non Knaf, nec Poir., nom. invalid.

B. lutarium Revel, Actes Soc. Linn. Bordeaux 25: 413, t. 4 (1865).

B. aquatile (L.) Dumort. var. *micranthum* (Wallr.) Kickx, Bull. Soc. Roy. Bot. Belg. 4: 219 (1865).

R. hydrocharis Spenner "form" *tripartitus* (DC.) Hiern, J. Bot. Lond. 9: 67 (1871), nom. invalid.

R. lutarius (Revel) Bouvet, Bull. Soc. Angers 96 (1874).

R. lenormandii F. Schultz proles *lutarius* (Revel) Rouy & Fouc., Fl. Fr. 1: 60 (1893).

R. lenormandii F. Schultz var. *intermedius* H. Cherm, sensu Sennen, Exsicc. Pl. Espagne no. 5219 (1915).

Icons

De Candolle, A. P. Icon. Pl. Gall. Rar. t. 49 (1808).

Cosson, E. & Germain, E. Atlas Fl. Env. Paris Pl. 1, fig. 7, 8 (1845).

Ross-Craig, S. Drawings of British Plants 1: 19 (1948).

Typification

The original description of *R. tripartitus* is accompanied by an adequate plate. It was described "in *Amorciae inundatis*". The only specimen in DE CANDOLLE'S herbarium at Genève (G) is of var. β *obtusiflorus* which was not described until 1817. Although it represents *R. tripartitus* sensu stricto it cannot be used as a type for the first or α element. The type specimen may be at the Museum National d'Histoire Naturelle, Paris (P), but until a specimen is found, I designate the plate and description in DE CANDOLLE'S *Icones Plantarum Galliae rariorum nempe incertarum aut nondum delineatarum* 15, t. 49 (1808) as a *typotype* (DANDY in STEARN 1957).

The nomenclature and typification of *R. obtusiflorus* and *R. petiveri* are discussed by COOK and PATZAK (1962). From the original description and plate *R. lutarius* is no more than the entire-leaved, terrestrial state of *R. tripartitus* but the name *R. lutarius* has frequently been used for the hybrid *R. tripartitus* X *omiophyllus*. This is described on page 187.

Description

Annual or perennial, prostrate in terrestrial state or spreading-erect under water. Leaves entire or divided into capillary segments. Entire leaves opposite or alternate; stipules suborbicular, adnate to petiole for more than $2/3$ their length, apex obtuse; petiole (10) 20 - 30 (70) mm long; lamina up to 40 mm wide, reniform to suborbicular, deeply 3- or rarely 5-lobed; lobes cuneate, distant; margin entire or crenate. Divided leaves confined to lower nodes or lacking, alternate; petiole 1 - 10 mm long; lamina 10 - 40 mm long, globoid to obconical; segments extremely fine, flaccid. Peduncles in fruit equal to or slightly shorter than petioles of the opposite entire leaves. Sepals 1 - 3 mm long, reflexed caducous, blue-tipped. Petals 1.25 - 4.5 mm long, ovate to slightly obovate, not contiguous; nectar-pits lunate. Stamens (1) 5 - 8 (10). Carpels 4 - 27, glabrous; style subterminal. Receptacle hairy.



Fig. 9.: Distribution of *R. tripartitus* (+ signifies a known extinction)

Distribution

R. tripartitus shows a distinctly Atlantic distribution (fig. 9) and throughout its range is generally considered a rare plant. There is evidence in the British Isles that it is contracting its range and in the last 60 years it has apparently become extinct in South Eastern England and Anglesey. In South East England the extinction is probably due to urban development and also lowering of the water table but in Anglesey it is more difficult to explain as its original habitat at Penhros Lligwy appears quite suitable when compared with its habitats at Arne and the Lizard.

Ecology

R. tripartitus has been studied in the field in Britain at The Lizard, Cornwall, and at Arne, Dorset. In these localities it is an ephemeral that behaves as a winter annual but in cultivation it is perennial. In nature it is found on peat at Arne and on soils with low calcium content at The Lizard (COOMBE and FROST 1956). Although it appears to be calcifuge it grows more vigorously on calcium rich soils in cultivation.

It is found on wet cart tracks, in ditches, temporary ponds and peaty pools. It starts flowering in March and usually dies during April or May. I think the reason for this early death in nature is due to its inability to compete with later growing aquatic plants such as *Apium inundatum*, *Scirpus fluitans* and *Ranunculus aquatilis* at The Lizard and *Peplis portula* and *Montia fontana* at Arne, or due to the habitat drying out. In a cool but frost-free greenhouse, without competing species flowering starts in February and ceases in September or November but when grown with *Peplis portula* it starts flowering in February but is usually dead by the end of May.

Variation

No significant genotypic variation has been detected in this species. The entire-leaved and heterophyllous states of this species are fairly distinct and have been described as belonging to different species. The entire-leaved state has often been called *R. lutarius* and differs from the heterophyllous state in that it is prostrate, frequently opposite-leaved, more vigorous, usually larger and later flowering. Some of the factors governing the production of these states are described on page 67 .

GLÜCK (1924) recognised and described four formae of *R. tripartitus* (*submersus*, *obtusiflorus*, *crenatus* and *terrestris*) and four formae of *R. lutarius* (*obtusilobus*, *crenulatus*, *amphibius* and *terrestris*). These formae are based on characters derived from more or less arbitrarily chosen size categories and leaf-shapes and have been seen on ramets of a single clone in cultivation. GLÜCK'S tables and descriptions (p. 253 - 258, 591 - 598) give a good impression of the limits of plasticity of this species.

4. *Ranunculus lobbii* (Hiern) A. Gray, Proc. Am. Acad. 21: 364 (1886).

R. hydrocharis Spenner "form" *lobbii* Hiern, J. Bot. Lond. 9: 66 (1871), nom. invalid.

R. hederaceus L. var. *lobbii* (Hiern) Brewer & Watson, Bot. Calif. 5 (1876), fide Drew, Rhodora 38: 16 (1936).

R. aquatilis L. var. *lobbii* (Hiern) S. Watson, Bibl. Ind. N. Amer. Bot. 17 (1878), fide Drew, loc. cit.

Batrachium lobbii (Hiern) Howell, Fl. N. W. Amer. 13 (1897), nom. legit.

B. lobbianum Gelert, Bot. Tidskr. 19: 34 (1894), appears in Index Kewensis as a synonym of *R. lobbii*. The work cited is about *batrachia* but this name is not mentioned.

Icones

Hiern, W. P., J. Bot. Lond. 9: t. 114 (1871).

Mason, H. L., Fl. Marshes California fig. 243 (1957).

Typification

The holotype of *R. lobbii* is at Kew Herbarium (K), collected from Oregon, U. S. A. by W. LOBB, number 249 (1852). I have examined this specimen. It is well preserved and representative of the species.

Description

Annual or perhaps perennial, prostrate in terrestrial state, spreading-erect under water. Leaves entire or divided into capillary segments. Entire leaves alternate; stipules suborbicular, adnate to petiole for more than $\frac{2}{3}$ their length, apex obtuse; petiole up to 40 mm long; lamina up to 12 mm wide, reniform to suborbicular, deeply 3- or rarely 5-lobed; lobes cuneate, distant; margin entire or crenate. Divided leaves confined to lower nodes or absent, alternate; petiole 5 - 20 mm long; lamina globoid to obconical; segments fine, flaccid. Peduncles in fruit more or less equal to petiole of opposed entire leaf. Sepals 2 - 3 mm long, spreading, caducous, blue-tipped. Petals 4 - 6 mm long, ovate to obovate, not contiguous; nectar-pits lunate. Stamens 5 - 16. Carpels 2 - 6, 2.5 mm long, glabrous; style subterminal to lateral, 1.5 mm long at anthesis, caducous. Receptacle glabrous.

Distribution

The coastal areas of North West America from San Francisco to Vancouver Island (fig. 10).

Ecology

I have not seen living material of this species but personal communications from L. BENSON (Pomona) and S. COOK (Oregon) indicate that *R. lobbii* is ecologically very similar to *R. tripartitus* being found in ephemeral, vernal pools.

Variation

From the limited quantity of herbarium material examined *R. lobbii* appears to show surprisingly little variation. The divided leaves are very fine and may be missing. The carpel number is very constant and remarkably low, never exceeding 6. Apart from the low carpel number and glabrous receptacle *R. lobbii* closely resembles *R. tripartitus* and I feel there is a close patristic relationship between them.



Fig. 10.: The distribution of *R. lobbiai* (Western North America).

5. Ranunculus ololeucos Lloyd, Fl. Loire-Inf. 3 (1844).

Batrachium ololeucos (Lloyd) Van den Bosch, Prodr. Fl.
Batav. 1: 6 (1850), nom. legit.

R. paucicarpus Arv. -Touv., Essai Pl. Dauph. 17 (1871).

R. lusitanicus Freyn, Flora (Regensb.) 63: 24 (1880).

B. lusitanicum (Freyn) Nyman, Consp. Fl. Eur. Suppl. 1:
10 (1883).

Icones

Cosson, E. & Germain, E. Atlas Fl. Env. Paris pl. 1, fig. 5, 6
(1845).

Glück, H. Wasser- und Sumpfgewächse 4: t. 4, fig. 1 - 5 (1924).

Typicifaction

I have not seen type material of this species but it should be at the Museum National d'Histoire Naturelle, Paris (P). I have seen material of *R. ololeucos* collected and determined by LLOYD, in the herbaria at Kew (K) and Coimbra (COI). I have seen isotype material of *R. lusitanicus* in Kew (K) and Coimbra (COI).

Description

Annual or perennial, prostrate in terrestrial state spreading erect under water. Leaves entire or divided into capillary segments. Entire leaves opposite or alternate; stipules suborbicular, adnate to petiole for more than $\frac{2}{3}$ their length, apex obtuse; petiole (20) 40 - 60 (100) mm long; lamina up to 30 mm wide, reniform to suborbicular, deeply 3- or rarely 5-lobed; lobes cuneate, distant; margin entire or crenate. Divided leaves rarely lacking, alternate; petiole 1 - 40 mm long; lamina 10 - 50 mm long, obconical to globoid; segments when submerged extremely fine, flaccid, when emergent flattened, rigid. Peduncles in fruit equal to or slightly longer than petioles of opposed entire leaves. Sepals 3.5 - 4.5 mm long, reflexed, occasionally blue-tipped. Petals 7 - 15 mm long, ovate to slightly obovate, not contiguous; nectar-pits lunate. Stamens (10) 15 - 20 (25). Carpels 16 - 30, glabrous; style subterminal. Receptacle hairy.



Fig. 1.: The distribution of *R. ololeucos*.

Distribution

Western Europe from Portugal to the Netherlands but absent from the British Isles (fig. 11).

Ecology

I have only seen this species once from Maarn, near Utrecht, Holland. It was growing in a sandstone area in an oligotrophic dyke about 20 cm deep and was the only Angiosperm present. This habitat resembles the type of habitat that supports *R. tripartitus* in Cornwall, England, and I would judge that *R. ololeucos* is ecologically very similar to *R. tripartitus*.

R. ololeucos is considered a very rare plant in Holland and is only known from one other locality.

Variation

GLÜCK (1924) recognised five formae (*typicus*, *rotundilobus*, *schizolobus*, *submersus* and *terrestris*). These formae have all been seen on ramets of the single plant "O1-1" (see p. 56).

The plastic responses of *R. ololeucos* closely parallel those of *R. tripartitus* with the exception that divided leaves are found on terrestrially cultivated plants during short photoperiods (p. 67) and that entire-leaved stems will revert to divided-leaved ones after exposure to long photoperiods. In general, *R. ololeucos* may be regarded as exhibiting less vigour in a terrestrial state than *R. tripartitus* but more vigour than *R. tripartitus* in an aquatic state. Both species are essentially amphibious but *R. ololeucos* is dominantly aquatic while *R. tripartitus* is dominantly terrestrial.

R. ololeucos possesses two strains, one with entirely white petals found throughout the range of the species and the other with yellow clawed petals that is confined to North Spain and Portugal. This yellow clawed strain has been called *R. lusitanicus* but as it is sympatric with *R. ololeucos*, I feel it is not worth taxonomic recognition at specific or subspecific rank.

6. Ranunculus baudotii Godron, Mém. Soc. Roy. Nancy 1839: 21 (1840).

R. petiveri Koch in Sturm, Deutschl. Fl. 82, t. 2 (1840)
pro parte.

Batrachium marinum Fr., Nov. Fl. Seuc. 3:5 (1842).

R. marinus (Fr.) Hartm., Handbk. Skand. Fl. ed. 4, 179 (1843).

R. petiveri Koch var. major Koch, Syn. Fl. Germ. ed. 2, 13 (1843).

B. baudotii (Godron) F. Schultz, Arch. Fl. Fr. & Allem. 71 (1844), nom. legit.

B. petiveri (Koch) F. Schultz, loc.cit.

R. confusus Godron in Gren. & Godron, Fl. Fr. 1: 22 (1847).

R. kochii Beurl., Bot. Notiser 156 (1852), non Ledeb.

R. friesii Beurl., loc.cit.

B. confusum (Godron) Garcke, Fl. Nord-Mittel-Deutschl. ed. 4, 7 (1858).

R. aquatilis L. var. symei Hooker & Arn., Brit. Fl. ed. 8, 7 (1860).

R. heterophyllus Weber subsp. baudotii (Godron) Moore & More, Cybele Hibernica 5 (1866).

R. hydrocharis Spenner "form" baudotii (Godron), "form" confusus (Godron) Hiern, J. Bot. Lond. 9: 66 (1871), nom. invalid.

R. marinus (Fr.) Hartm. subsp. baudotii (Godron) subsp. confusus (Godron) Hayward, Hayward's Botanists Pocket Book ed. 5, Appendix (1886).

R. gelertii E. H. L. Krause in Sturm, Fl. Deutschl. ed. 2, 5: 267 (1901).

R. obtusiflorus (DC.) Moss, J. Bot. Lond. 52: 114 (1914).

Icones

Godron, C., Mém. Soc. Roy. Nancy 1839: fig. 4 (1840).

Glück, H., Wasser- und Sumpfgewächse 4: t. 3, fig. 4 - 9 (1924).

Ross-Craig, S., Drawings of British Plants 1: 18 (1948).

Typification

I have not seen the holotype which should be in the herbarium of L'Institut Botanique de Faculté des Sciences, Nancy (NCY), "In rivulis propre Sarrebourg, Comm. BAUDOT" but I have seen isotypes at Kew (K) and Edinburgh (E). The nomenclature of *R. baudotii* has been discussed by MOSS (1914) and COOK and PATZAK (1962).

Description

Annual or perennial, prostrate in terrestrial state or spreading-erect under water. Leaves entire or divided into capillary segments. Entire leaves occasionally lacking, alternate; stipules suborbicular to orbicular, adnate to petiole for more or less $1/2$ their length, apex obtuse; petiole up to 80 mm long; lamina up to 30 mm wide; reniform to suborbicular, often truncate at base, deeply 3- or rarely 5-lobed; lobes cuneate, sinus more than $2/3$ as long as lobe; margin crenate or rarely dentate. Divided leaves always present, alternate; petiole 5 - 20 mm long; lamina obconical to subglobose; segments rigid, divergent. Leaves intermediate between entire and divided occasionally present. Peduncles in fruit longer than petiole of opposed entire leaf. Sepals 2.5 - 4.5 mm long spreading or reflexed, usually blue-tipped. Petals 5.5 - 10 mm long, broadly obovate, contiguous during anthesis; nectar-pits lunate. Stamens 10 - 20. Carpels (16) 33 - 39 (60), glabrous, winged when dry; receptacle hairy, elongating in fruit.

Distribution

R. baudotii is found in coastal districts in most of Europe south of 65° N and in Western North Africa (fig. 12). It has been reported from several inland areas but the only records supported by herbarium material that I have found are from Sarrebourg, France and Burgenland, Austria.

Ecology

R. baudotii is found in coastal districts (or near salt deposits) on mud flats or in brackish ditches. It is usually found in open and disturbed habitats. It is very tolerant of salt water



Fig. 12.: Distribution of *R. baudotii*.

and one population at Brading, Isle of Wight, England, was found that was covered by sea water at high tide. In Britain it rarely roots more than 30 cm below the surface of the water and usually grows rooted on the bank spreading over the water or as a terrestrial plant. In cultivation it will not tolerate depths of more than 1 m and if planted deeper it becomes uprooted and floats to the surface. LUTHER (1951), however, has reported it in 3 m of clear brackish water in Finland.

Adopting the classification of OLSEN (1950), LUTHER (1951) assigns *R. baudotii* in Finland to the Oligo- β -mesohaline group which means that it is an obligate brackish water species found in a salinity range of 1 - 6 parts per thousand and often associated with plants such as *Zostera marina*, *Ruppia spiralis* and *Chara baltica*. In Finland he also reports this species as tolerating most substrata from mud to gravel, resistant to wave action and water currents, overwintering under ice as a green plant and spreading effectively by seed. LUTHER has kindly sent me material from Finland (plant B-4) and when cultivated at München and Liverpool was found to behave substantially the same as Western European material and grew vigorously in fresh water and would not tolerate depths of more than 1 m.

All strains of *R. baudotii* kept in cultivation (B-1, B-2, B-3, B-4) were found to grow vigorously in fresh water; as this species seems to be confined to salt water in nature and investigation was undertaken to compare its behaviour with other species in different concentrations of sea water. Equal-aged, four node, rooted cuttings of *R. baudotii* (B-2) and *R. aquatilis* (A-6) in a divided-leaved state were placed in a set of paired aquarium tanks 40 cm deep filled with distilled water, 5 %, 10 %, 50 % and 100 % sea water. All plants were potted in John Innes No. 1 compost and were previously conditioned in fresh water. The experiment was carried out in a cool greenhouse at Cambridge and started on 8th April, 1959.

After 41 days, both species in distilled water had put on very little new growth and were looking weak. In 5 % sea water both species were growing well, had reached a heterophyllous state and were flowering and fruiting. In 10 % sea water they were both in a heterophyllous state with flowers and fruits but *R. baudotii* was more robust. In 50 % sea water *R. baudotii* was robust but slow-growing and had only the first flowers and entire

leaves while *R. aquatilis* was very weak and was in a divided-leaved state without flowers (it died soon after). In 100 % sea water *R. baudotii* was just alive while *R. aquatilis* had died 22 days before. *R. aquatilis* grew surprisingly well in sea water but in concentrations of more than 5 % *R. baudotii* showed more vigour and a better tolerance to sea water.

The flowering time of *R. baudotii* throughout its range is from March to September but in any particular locality it is very variable and dependant on local conditions.

Variation

R. baudotii is usually found in open and disturbed habitats and exhibits considerable phenotypic plasticity. In the Baltic region it frequently grows in permanent water as a submerged plant and often flowers and fruits without developing entire leaves. This divided-leaved state has been given specific rank and named *R. marinus*. LUTHER (1947) examined this species in some detail in Finland and came to the conclusion that *R. marinus* was merely a local habitat-induced modification of *R. baudotii*.

In West and South Europe *R. baudotii* is usually heterophyllous in summer and divided-leaved in winter. Occasionally entire-leaved portions of stem become detached in summer and although they are annual they may continue growing for several weeks. Roots are rare on these stems and as they grow they become less robust and develop smaller flowers and deeply 3-lobed leaves. These detached stems have often been misidentified as *R. tripartitus*.

GLÜCK (1924) recognised five varieties and five formae but in 1936 he reorganised the ranks of these taxa to three varieties, three formae and four sub-formae. These taxa are based on various manifestations of the divided-leaved, heterophyllous and terrestrial states of *R. baudotii*. The descriptions and tables in GLÜCK (1924 p. 234 - 243) give a good overall impression of the range of phenotypic plasticity met with in this species.

R. baudotii does exhibit some genecological differentiation and when the plants B-2 from England, B-3 from Austria and B-4 from Finland are cultivated side by side under uniform conditions at Liverpool various differences can be detected but they are quantitative and no sharp distinctions can be made. For example, when cultivated in 25 cm of water the English plant

usually develops entire leaves earlier than the others and is generally more robust. In early summer the entire leaves of the three strains are 3-lobed and reniform in outline and look alike but towards the end of the summer the English plant develops 5-lobed, suborbicular leaves while the leaves of the other plants usually remain 3-lobed and reniform. When cultivated terrestrially the Austrian plant develops only divided leaves while the others develop divided and intermediate leaves; the Finnish plant develops more intermediate leaves than the English plant. These differences apparent from cultivation experiments in Britain are not, however, consistent with differences seen when these plants grow in their natural localities.

7. Ranunculus saniculifolius Viv., Fl. Lib. 29 (1824).

R. tenellus Viv., Pl. Aegypt. 6 (1831).

Batrachium saniculifolium (Viv.) Dumort., Bull. Soc. Bot.
Belg. 2: 211 (1863), nom. legit.

B. tenellum (Viv.) Dumort. loc. cit.

R. hydrocharis Spenner "form" saniculifolius (Viv.) Hiern,
J. Bot. Lond. 9: 66 (1871), nom. invalid.

? R. atlanticus Pomel, Nouv. Mat. Fl. Atl. 248 (1874) non
Ball.

? R. fucoides Freyn in Willk. & Lange, Prodr. Fl. Hisp.
3: 912 (1880).

R. macranthus Tod., Fl. Sic. exsicc. no. 1167 (1882).

R. aquatilis L. var. baudotii Crépin, Man. ed. 5, 10 (1884).

R. vespertilio Lojac., Fl. Sic. 33, t. 3 (1888).

R. aquatilis L. var. macranthus (Tod.) Lojac., Fl. Sic. 35,
t. 4 (1888).

R. pomelianus Debeaux, in Reverchon, Exsicc. Pl. Algerie
(1897), nom. in Schaed. no. 229.

R. rodiei Maire, Pl. Maroc. exsicc. no. 868 (1924), nom.
in Schaed.

Icones

Viviani, D., *Florae Libycae Specimen* t. 2, fig. 2 (1824).

Lojacono-Pojero, M., *Flora Sicula* 1: t. 3 (1888).

Typification

After his original description VIVIANI describes the species from "in inundatis salis, Magnae Syrteos" (Sirte in Libya). VIVIANI'S collection of specimens was kept at Genoa (GE) but was unfortunately destroyed during the second world war. Some of VIVIANI'S duplicates were incorporated into BERTOLONI'S herbarium and are now at Bologna (BOLO) but I do not know if any specimens of *R. saniculifolius* are still in existence.

Description

Annual or perhaps perennial, prostrate in terrestrial state, spreading erect under water. Leaves entire or divided into capillary segments. Entire leaves alternate; stipules suborbicular, adnate to petiole for more than $2/3$ their length, apex obtuse; petiole up to 40 mm long; lamina up to 12 mm wide, reniform to suborbicular, deeply 3- or rarely 5-lobed; lobes cuneate, distant; margin entire or crenate. Divided leaves confined to lower nodes or lacking, alternate; petiole 5 - 20 mm long; lamina globoid to obconical; segments fine, flaccid. Peduncles in fruit more or less equal to petioles of opposed entire leaves. Sepals 2 - 3 mm long, spreading, caducous, blue-tipped. Petals 4 - 6 mm long, ovate to obovate, not contiguous; nectar-pit lunate. Stamens 5 - 16. Carpels 2 - 6, 2.5 mm long, glabrous; style subterminal to lateral, 1.5 mm long at anthesis, caducous. Receptacle glabrous.

Distribution

In coastal districts scattered throughout the Mediterranean region (fig. 13).

Ecology & Variation

I have failed to see *R. saniculifolius* in the field and am indebted to D. MEIKLE (Kew) for a description of its ecology in Cyprus and for living material. It is a very short-lived annual found in ephemeral pools. It grows in both brackish and fresh water and is rarely found more than 15 km away from the sea.



Fig. 13. : Distribution of *R. saniculifolius*.

In cultivation seeds germinate readily but it is a difficult plant to raise as it seems very susceptible to fungal attack and is also readily eaten by snails and slugs. It is remarkably stenoplastic and the change from divided to capillary leaves seems to be an endogenous heteroblastic development (page 68). Morphologically, *R. saniculifolius* is intermediate between *R. baudotii* and *R. peltatus* but its plastic responses are very different from these two species. I believe that this difference is due to ecological specialisation, as *R. saniculifolius* is not ecologically sympatric with either *R. baudotii* or *R. peltatus* and that these three species show close patristic affinities.

8. *Ranunculus peltatus* Schrank, Baier. Fl. 2: 103 (1789).

Batrachium aquatile (L.) var. *peltatum* (Schrank) Dumort.,
Fl. Belg. 127 (1827).

R. hydrocharis A, *heterophyllus* var. *vulgaris* var. *peltatus* (Schrank) Spenner, Fl. Frib. 4: 1008 (1829)
nom. invalid.

- R. aquatilis* L. var. *peltatus* (Schrank) var. *quinqulobus*
var. *truncatus* Koch, Syn. Fl. Germ. 11. (1835).
- ? *R. aquatilis* L. var. *heterophyllus* Moris, Fl. Sard.
25 (1837).
- R. petiveri* var. *major* Koch, Syn. Fl. Germ. ed. 2, 13
(1843), pro parte.
- R. floribundus* Bab., Ann. & Mag. Nat. Hist. ser. 2, 16:
397 (1855).
- R. rhipiphyllus* Bast. in Boreau, Fl. Centr. Fr. ed. 3, 2:
11 (1857).
- R. aquatilis* L. var. *subpeltatus* Hooker, Stud. Fl. Brit.
Isles ed. 8, 7 (1860).
- B. heterophyllum* (Moris) Lange, Pugill. Plant. 251 (1860-
1865), nom. invalid.
- B. rhipiphyllum* (Bast.) Dumort., Bull. Soc. Bot. Belg. 2:
211 (1863), nom. legit.
- B. truncatum* (Koch) Dumort., loc. cit.
- R. heterophyllus* Weber subsp. *peltatus* (Schrank) Moore
& More, Cybele Hibernica 5 (1866).
- R. elongatus* F. Schultz, Billota 113 (1869).
- R. hydrocharis* Spenner "form" *elongatus* (F. Schultz)
"form" *floribundus* (Bab.) "form" *rhipiphyllus* (Bast.)
"form" *triphyllus* (Wallr.) pro parte, "form"
truncatus (Koch) Hiern, J. Bot. Lond. 9: 97 - 99
(1871), nom. invalid.
- B. dichotomum* Schmalh., Trav. Soc. Nat. St. Pétersb. 5:
(1874), fide Krecz. in Komarov 7: (1937).
- B. langei* F. Schultz in Nyman, Consp. Fl. Eur. 16 (1878).
- B. trinacrium* (Huet) Nyman, loc. cit.
- B. cesatianum* Caldesio, Nuovo Gior. Bot. Ital. 11: 324
(1879).
- R. dubius* Freyn in Willk. & Lange, Prodr. Fl. Hisp. 3: 909
(1880).
- R. leontinensis* Freyn in Willk. & Lange, loc. cit.

- R. baudotii* subsp. *leontinensis* (Freyn) Nyman, Suppl.
Consp. Fl. Eur. 10 (1883).
- B. aquatile* (L.) Dumort. var. *grandiflorum* Groves, Nouvo
Giorn. Bot. Ital. 19: 120 (1887).
- R. aquatilis* L. var. *elegans* var. *elongatus* (Hiern)
A. Chabert, Bull. Soc. Bot. Fr. 36: 15 (1889).
- R. diversifolius* Gilib. proles *floribundus* (Bab.), proles
peltatus (Schränk), proles *truncatus* (Koch) Rouy &
Fouc., Fl. Fr. 1: 64 (1893), nom. invalid.
- R. diversifolius* Gilib. var. *rhizophyllum* (Bast.) Félix,
Bull. Soc. Bot. Fr. 58: 97 - 104 (1911), nom. invalid.
- R. longecapillatus* Sennen, Pl. Espagne 10 (1936).

The following names are difficult to apply but belong to
heterophyllous plants that could be either *R. peltatus* or
R. aquatilis.

- R. aquaticus* Lam., Fl. Fr. 3: 184 (1778), nom. invalid.
- R. diversifolius* Gilib., Fl. Lithuan. 5: 262 (1782), nom.
invalid.
- B. heterophyllum* S. F. Gray, Nat. Arr. Brit. Pl. 2: 98 (1821),
nom. invalid.
- R. triphyllus* Wallroth, Linnaea 14: 584 (1840).
- R. intermedius* Knaf, Flora (Regensb.) 29: 289 (1846) non
Eaton, nec Poir., nec Schur.
- B. triphyllus* (Wallroth) Dumort., Bull. Soc. Bot. Belg. 2:
214 (1863).
- R. eleophilus* Arv. -Touv., Essai Pl. Dauph. 19 (1871).
- B. paucistamineum* (Tausch) F. Schultz var. *diversifolium*
(Gilib.) Gelert, Bot. Tidsskr. 19: 27 (1894).

The following names apply to the divided-leaved state of
R. aquatilis or *R. peltatus*.

- R. aquatilis* L. var. *submersus* Gren. & Godron, Fl. Fr. 1:
23 (1847).

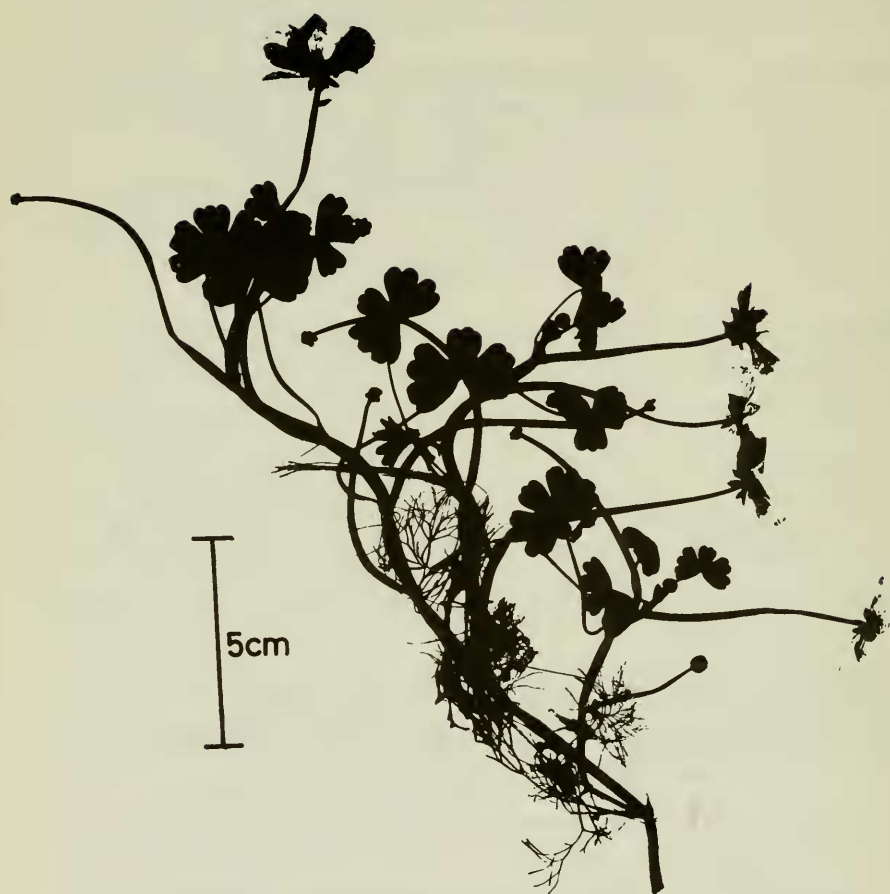


Fig. 14. : *R. peltatus*.

R. submersus (Gren. & Godron) Godron, Bull. Soc. Bot. Fr.
6: 498 (1859).

Icones

Ibid figure 14.

Typification

SCHRANK'S original diagnosis is insufficient but he mentions a specimen collected by Dr. VON POSCHINGER from Közting. In SCHRANK'S herbarium at München this specimen has not been found but among his material is a well preserved and adequate specimen of *R. peltatus* collected by FRÖLICH and bearing the name *R. peltatus*. SCHRANK and FRÖLICH were friends and some of FRÖLICH'S specimens were used as types by SCHRANK. In the absence of VON POSCHINGER'S specimen I designate the specimen collected by FRÖLICH in the herbarium, Staatssammlung München (M) the neotype of *R. peltatus*.

Description

Annual or perennial, caespitose in terrestrial state or spreading-erect under water. Leaves entire or divided into capillary segments. Entire leaves occasionally lacking, alternate; stipules oblong to triangular, adnate to petiole for $\frac{3}{4}$ or more their length, apex obtuse; petioles rarely exceeding 70 mm long; lamina up to 40 mm wide, reniform to obicular, occasionally 3- or 7-lobed; lobes broadly cuneate, sinus usually less than $\frac{2}{3}$ the length of the lamina; margin crenate. Divided leaves mostly present, alternate; petiole 5 - 25 mm long; lamina globose to obconical; segments rigid or flaccid, divergent. Leaves intermediate between entire and divided very rare. Peduncles in fruit rarely less than 50 mm long, longer than petiole of opposed entire leaf. Sepals 3 - 6 mm long, spreading caducous. Petals (9) 12 - 15 (21) mm long, broadly obovate, contiguous during anthesis; nectar-pits elongate more or less pyriform. Stamens 15 - 30. Carpels (25) 30 - 40 (80), hairy when immature, occasionally glabrous when mature; style lateral to subterminal. Receptacle hairy, remaining globose in fruit.

Distribution

R. peltatus is confined to Europe and the coastal region of North Africa. It occurs throughout Europe except for the



Fig. 15.: Distribution of *R. peltatus* (eastern limits from Komarov, Fl. URSS.).

greater part of the Volga basin and the extreme north of Scandinavia. Figure 15 shows the distribution of this species.

Ecology and Variation combined with *R. trichophyllus* (page 134).

9. *Ranunculus sphaerospermus* Boiss. & Blanche in Boiss.,
Diagn. Pl. Or. Nov. 3(5): 6 (1856).

R. aquatilis L. var. *sphaerospermus* (Boiss. & Blanche)
Boiss., Fl. Or. 1: 23 (1867).

R. peltatus Schrank subsp. *sphaerospermus* (Boiss. & Blanche) Meikle, Notes Roy. Bot. Gard. Edin. 23: 16 (1959).

B. rhipiphyllum subsp. *sphaerospermum* (Boiss. & Blanche) C. D. K. Cook, Mitt. Bot. München 3: 600 (1960), nom. legit.

Typification

I have seen an isotype at Kew (K). "Syria in paludosis marivicinis, circa Tripolin et Alexandrette. Coll. BLANCHE."

Description

Annual, caespitose in terrestrial state, spreading-erect under water. Leaves divided into capillary segments, entire leaves absent; stipules oblong to triangular, adnate to petiole for half or more their length; petiole up to 20 mm long; lamina globose; segments semi-rigid, divergent. Peduncles in fruit (30) 50 - 60 (80) mm long. Sepals 3 - 6 mm long, spreading, caducous. Petals 9 - 25 (30) mm long, broadly obovate, contiguous during anthesis; nectar-pits more or less pyriform. Stamens 15 - 25. Carpels 50 - 80, less than 1 mm long, more or less globose, glabrous or slightly hairy at base of style; style lateral to subterminal. Receptacle hairy, elongating in fruit.

Distribution

Figure 16 shows the distribution of *R. sphaerospermus*. It occurs in E. Greece, Asia Minor, Kashmir and Nepal and is allopatric with *R. peltatus*.

Ecology & Variation

I have not seen *R. sphaerospermus* in the field but according to P. H. DAVIS (Edinburgh) and R. D. MEIKLE (Kew) it is found in ephemeral pools or permanent pools with fluctuating water levels and is ecologically similar to *R. rionii*. I have seen mixed gatherings of these two species and assume they occasionally grow intermingled.

In cultivation its behaviour is similar to *R. peltatus* except that it is annual and never develops entire leaves. When submerged it has long petioles in winter and short ones in summer. The peduncle length is highly plastic and may be as long



Fig. 16.: The distribution of *R. circinatus* (dotted line), *R. sphaerospermus* (circular dots) and *R. flavidus* (triangular dots).

as 8 cm if the plant is kept submerged in 40 cm of water or as short as 3 cm if the plant is cultivated terrestrially. The terrestrial state can be cultivated only under a regime of long photo-periods.

10. *Ranunculus aquatilis* L., Sp.Pl. 556 (1753).

R. heterophyllus Weber in Wigg. Prim. Holst. 42 (1790).

R. peltatus Moench, Methodus 214 (1794), non Schrank,
nom. invalid.

R. aquatilis L. var. *heterophyllus* (Weber) DC. in Lam. &
DC., Fl. Fr. 4: 984 (1805).

Batrachium peltatum (Moench) Bertch. & Presl., Rostl. 49
(1823), nom. invalid.

R. radians Revel, Renonc. Gironde fig. 1, 8 (1845), fide
Revel, Actes Soc. Linn. Bordeaux (1853).

- R. tripartitus Kittel, Fl. Deutsch. 254 (1847), non DC.,
nom. invalid.
- B. godronii Gren., Fl. Gall. & Germ. Exsicc. no. 1202
(1848).
- R. hypotrichus Turcz., Bull. Soc. Nat. Moscou 2: 275 (1854).
- B. radians (Revel) Desmoulins, Actes Soc. Linn. Bordeaux
20 (1859).
- B. aquatile (L.) Dumort., Bull. Soc. Bot. Belg. 2: 215
(1863).
- R. hydrocharis Spenner "form" radians (Revel), godronii
(Gren.) Hiern, J. Bot. Lond. 9: 99 (1871), nom.
invalid.
- R. circinnatoides Arv. -Touv., Essai Pl. Dauph. 18 (1871).
- R. allophyllus Bast., Exsicc. Soc. Dauph. no. 1069, fide
Arv. -Touv. loc. cit.
- B. carinatum Schur, Verh. Nat. Ver. Brünn 15: 2 (1876).
- R. leiospermus Hartm., Scand. Fl. ed. 11, 165 (1879).
- R. carinatus (Schur) Freyn in Kern., Sched. Fl. Exsicc.
Aust. -Hung. 1: 21 (1881).
- R. grayanus Freyn, Deutsch. Bot. Monatschr. 8: 179 (1890).
- R. trichophyllus Chaix var. radians (Revel), var. godronii
(Gren.) Rikli in Schinz & R. Keller, Fl. Schweiz 193
(1900).
- R. virzionensis Félix, Bull. Soc. Bot. Fr. 59: sess. extr.
63 (1912).
- R. longifolius (Rossm.) Hegi, Ill. Fl. Mitteleur. 3: 581
(1912).
- R. paui Sennen, Monde Pl. 29: no. 173, 6 (1928).
- R. trichophyllus Chaix var. hispidulus (E. R. Drew) W. B.
Drew, Rhodora 38: 29 (1936).
- R. nipponicus (Makino) Nakai, Bot. Mag. Tokyo 42: 19
(1928).
- R. aquatilis L. subsp. mongolicum Kryl., Fl. Zap. Sib. 5:
1180 (1931).

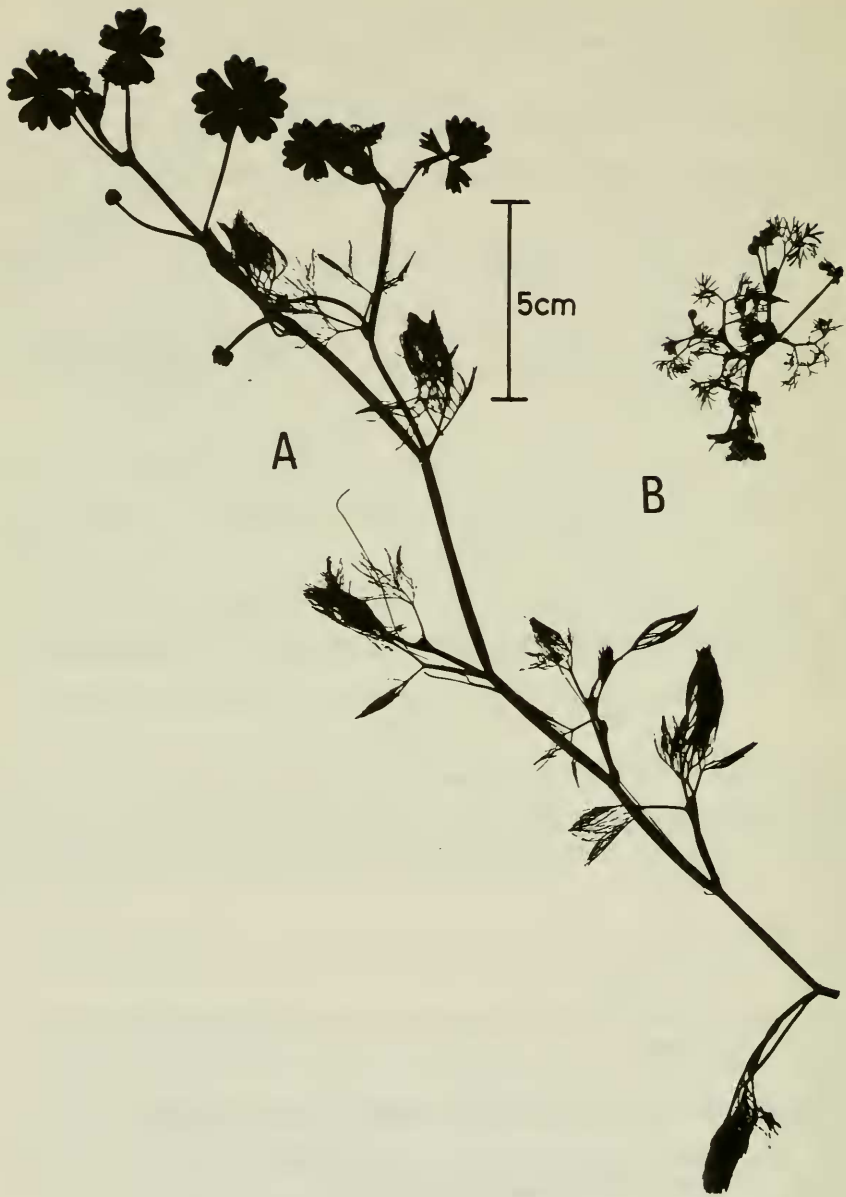


Fig. 17.: *R. aquatilis* — A) aquatic state, B) terrestrial state

B. mongolicum (Kryl.) Krecz. in Komarov, Fl. URSS.
7: 337 (1937).

B. gilibertii Krecz. in Komarov, Fl. URSS. 7: 336 (1937).

Icones

Ibid figure 17.

Typification

Sheet number 73 in the Linnaean Herbarium Linnean Society, London (LINN) bears a well preserved and adequate specimen of *R. aquatilis*. There are two other specimens in the herbarium, sheet number 76 has a specimen lacking entire leaves and the one on sheet number 77 has only stems and immature fruits.

The original diagnosis of *R. aquatilis* is "*RANUNCULUS foliis submersis capillaceus, emersis peltatis*". None of the batrachian or other ranunculi have peltate leaves, even in the sense employed by LINNAEUS (*Philosophica Botanica* 1751). The entire leaves of *R. aquatilis* are lobed and with an overall shape that is reniform to suborbicular. The use of "*peltatis*" is undoubtedly an error as in the second edition of the *Species Plantarum* 781 (1762), LINNAEUS changed the diagnosis to "*RANUNCULUS foliis submersis capillaceus, emersis sub-peltatis*".

JACKSON (1912) stated that sheet number 75 did not reach the Linnaean Herbarium until 1767, too late for the second edition of *Species Plantarum*. There is no complete specimen in *Hortus Cliffortianus* and BENSON (1954) did not find any authentic type material at Naturhistoriska Riksmuseum, Stockholm (S), or in the Burser Herbarium at the University of Uppsala (UPS). Although JACKSON'S dating of Linnaean specimens is suspect, I feel it is safer to designate the specimen on sheet number 75 (LINN) a neotype.

Description

Annual or perennial, caespitose in terrestrial state or spreading-erect under water. Leaves entire or divided into capillary segments. Entire leaves occasionally lacking, alternate; stipules triangular adnate to petiole for $3/4$ or more their length; petiole up to 90 mm long; lamina up to 30 mm wide, reniform to orbicular, 5- or occasionally 3- or 7-lobed; lobes broadly cuneate, sinus usually less than $2/3$ the length of the lamina; margin den-



Fig. 18. : The distribution of *R. aquatilis*.

tate. Divided leaves invariably present, alternate; petiole up to 25 mm long; lamina globoid; segments rigid or flaccid, divergent. Leaves intermediate between entire and divided rare. Peduncles in fruit rarely exceeding 50 mm, shorter than the petiole of the opposed entire leaf. Sepals 3 - 5 mm long, spreading, caducous. Petals 5 - 10 mm long, broadly obovate, contiguous during anthesis; nectar-pits circular, more or less cup-shaped. Stamens 14 - 22. Carpels (21) 32 - 36 (49) hairy when immature, occasionally glabrous when mature; style subterminal. Receptacle hairy, remaining globose in fruit.

Distribution

In the Old World *R. aquatilis* occurs almost throughout Europe except in the extreme north, and in North Africa, the Altai region of Mongolia, North and West China and Japan. In the New World it is confined to the west between latitudes 50° - 30° North and 10° - 75° South (fig. 18). In tropical South America it is confined to the Andes between 2,700 m and 4,000 m altitude.

Ecology & Variation combined with *R. trichophyllus* (page 134).

11. *Ranunculus flavidus* (Hand.-Mazz.) C. D. K. Cook, *Watsonia* 5: 297 (1963).

Batrachium flavidum Hand.-Mazz., *Acta Horti Gothob.* 13: 168 (1939), nom. legit.

Typification

The holotype is at Uppsala (UPS). "China: Sze-ch'uan boreo-occid. HARRY SMITH, NO. 4236." I have seen photographs of the holotype and isotypes at Edinburgh (E) and Wien (W).

Herbarium specimens seen

China: Sze-ch'uan boreo-occid. HARRY SMITH, No. 4236. UPS!
W!

China: Kansu, Chung-wei. R. C. CHING, No. 228. E!

Kashmir: Ladak, Shunshal. KOELZ, No. 2442. E!

Kashmir: Spitug, KOELZ, No. 2678a. E!

Description

Leaves divided into capillary segments, entire leaves absent; stipules oblong to triangular, adnate to petiole for $\frac{3}{4}$ or more their length; petiole up to 10 mm long; lamina globoid to obconical; segments flaccid. Peduncle in fruit up to 80 mm long. Sepals 4 - 5 mm long, reflexed, caducous. Petals 8 - 10 mm long, pale yellow, obovate, contiguous at early anthesis becoming separate later; nectar-pits lunate. Stamens more or less 20. Carpels approximately 20 - 40, glabrous (no mature specimens have been seen but the isotype at Wien (W) suggests that the carpels may be small, similar to *R. sphaerospermus* and *R. rionii*); style lateral to subterminal. Receptacle hairy.

Distribution

R. flavidus is known only from two localities in W. China and two localities in Kashmir (fig. 16).

Ecology & Variation

No living material of *R. flavidus* has been seen. From herbarium specimens its flowering time is from June to September and its altitudinal range from 2,400 m to 4,400 m. The petals are a uniform pale yellow colour, otherwise this species closely resembles *R. aquatilis* in a divided leaved state.

12. *Ranunculus trichophyllus* Chaix in Villars, Hist. Pl. Dauph. 1: 335 (1786), subsp. *trichophyllus*.

R. aquatilis L. subsp. *abrotanifolius* Ehrh., Hannover. Mag. 1780, 15: 225 (1780).

R. flaccidus Persoon, Ann. Bot. (Usteri) 14: 39 (1795).

R. aquatilis L. var. *diffusus* With., Arr. Brit. Pl. ed. 3, 2: 507 (1796).

R. aquatilis L. var. *phellandrifolius* Schum., Enum. Pl. Saell. 171 (1801).

R. fluviatilis Pursh, Fl. Amer. Sept. 2: 395 (1814).

- R. pectinatus* Dubois, Meth. Eprouvée ed. 2, No. 1030, 418 (1833), in syn. Gren. & Godron, Fl. Fr. 1: 24 (1848).
- Batrachium aquatile* (L.) Dumort. var. *trichophyllum* (Chaix) Spach, Hist. Nat. Vég. 7: 200 (1839).
- R. aquatilis* L. var. *brachypus* Hooker & Arn., Bot. Beech. Voy. pt. 7, Calif. Suppl. 316 (1840).
- R. aquatilis* L. var. *pantothrix* (Brot.) Koch in Sturm, Deutschl. Fl. t. 2, 67 (1840).
- R. abrotanifolius* (Ehrh.) Steudel, Nomencl. Bot. ed. 2, 2: 433 (1841).
- R. affinis* F. Schultz, Flora (Regensb.) 24: 558 (1841).
- R. drouetii* F. Schultz, Exsicc. Fl. Gall. & Germ. No. 404 (1841), Arch. Fl. Fr. & Allem. 10 (1842).
- R. minutus* Döll, Rhein. Fl. 550 (1843), fide Perrier & Songeon, Billot. Annot. 183 (1859).
- B. paucistamineum* (Tausch) F. Schultz, Arch. Fl. Fr. & Allem. 71 (1844), Exsicc. Fl. Gall. & Germ. No. 805 (1844).
- B. bipontinum* F. Schultz in Gren. & Godron, Fl. Fr. 1: 24 (1847).
- B. villosum* F. Schultz in Gren. & Godron, loc. cit.
- B. trichophyllum* Van den Bosch, Prodr. Fl. Batav. 1: 7 (1850), nom. legit.
- B. drouetii* (F. Schultz) Van den Bosch, loc. cit.
- B. aspergillifolium* Dumort., Bull. Soc. Bot. Belg. 2: 218 (1863).
- R. aquatilis* L. subsp. *trichophyllum* (Chaix) Moore & More, Cybele Hibernica 5 (1866).
- R. hydrocharis* Spenner "form" *trichophyllum* (Chaix) Hiern, J. Bot. Lond. 9: 101 (1871).
- R. microtorus* Arv. -Touv., Essai Pl. Dauph. 18 (1871).
- B. minimum* Schur, Verh. Naturf. Ver. Brünn 15: No. 2, 28 (1877), fide Index Kewensis.

- R. kaufmannii* Clerc, Bull. Soc. Oural. Amat. Sci. Nat. 4: 107 (1878).
- R. aschersonii* Freyn, Bot. Centr. 6: 15 (1881).
- R. curvirostris* Freyn, op. cit. 17.
- R. aquatilis* L. var. *drouetii* (F. Schultz) Lawson, Trans. Roy. Soc. Canada 2: 45 (1884).
- R. phellandrifolius* (Schum.) Krause, non vidi, in syn. Prahl., Krit. Fl. Prov. Schles. - Holst. 2: 4 (1890).
- R. hirtissimum* Krause, loc. cit.
- R. porteri* Britton, Bull. Torrey Bot. Club 17: 310 (1890).
- B. paucistamineum* (Tausch) F. Schultz var. *divaricatum* (Schrank), var. *drouetii* (F. Schultz) Gelert, Bot. Tidsskr. 19: 27 (1894).
- B. pedunculare* Green ex C. F. Baker, Leafl. Bot. Obs. Crit. 95 (1904).
- R. pseudoflaccidus* Petunn. Sir. Ill. Fl. Mosk. 153 (1907).
- B. porteri* (Britton) Britton in Rydb., Fl. Rocky Mts. & Adj. Plains 294 (1917).
- R. aquatilis* L. var. *bakeri* (Greene) var. *pedunculare* (Greene) Jepson, Man. Fl. Pl. Calif. 391 (1925).
- R. kazunsensis* Makino, J. Jap. Bot. 6: 8 (1929).
- B. kauffmannii* (Clerc) Krecz. in Komarov, Fl. URSS. 7: 343 (1937).
- R. aquatilis* L. var. *calvescens* (W. Drew) L. Benson, Bull. Torrey Bot. Club 69: 384 (1942).
- R. aquatilis* L. var. *porteri* (Britton) L. Benson, Am. Midl. Nat. 40: 236 (1948).
- R. aquatilis* L. var. *harrisii* L. Benson, loc. cit.

The following names refer either to *R. trichophyllus* or to specimens of *R. aquatilis* without entire leaves:

- R. pantothrix* Brotero, Fl. Lusit. 2: 375 (1804).
- R. paucistamineus* Tausch, Flora (Regensb.) 17: 525 (1834).

B. bakeri Greene, Leafl. Bot. Obs. Crit. 95 (1904).

The following names refer to terrestrial states which may be either *R. trichophyllum*, *R. aquatilis*, or *R. peltatus*:

R. caespitosus Thuill., Fl. Env. Paris ed. 2, 278 (1799)

R. pumilis Poir. in Lam., Encycl. Méth. Bot. 6: 133 (1804),
non Thuill.

R. aquatilis L. var. *caespitosus* (Thuill.) DC. in Lam.,
Fl. Fr. ed. 3, 4: 894 (1805).

B. caespitosum (Thuill.) S. F. Gray, Nat. Arr. Brit. Pl. 2:
722 (1821).

R. hydrocharis Spenner *B. homiophyllum* var. *caespitosus*
(Thuill.) Spenner, Fl. Frib. 4: 1008 (1829).

R. bauhini Tausch, Flora (Regensb.) 17: 525 (1834).

R. aquatilis L. var. *succulentus* Koch, Syn. Fl. Germ. &
Helv. 11 (1835).

The following are names that may refer to almost any species of *Batrachium* without entire leaves. The original diagnoses in all cases are insufficient and I have been unable to find any authentic specimens.

R. foeniculaceus Gilib., Fl. Lithuan. 4: 261 (1782), nom.
invalid.

R. divaricatus Schrank, Baier. Fl. 2: 104 (1789), nom.
invalid.

R. rigidus Persoon, Ann. Bot. (Usteri) 14: 39 (1795).

R. capillaceus Thuill., Fl. Env. Paris ed. 2, 278 (1799).

R. aquatilis L. var. *capillaceus* (Thuill.) DC. in Lam. &
DC., Fl. Fr. ed. 3, 4: 894 (1805).

B. capillaceum (Thuill.) Bercht. & Presl., Rostl. 49 (1823).

B. rigidum (Persoon) Dumort., Fl. Belg. 127 (1827).

R. hydrocharis Spenner *B. homiophyllum* var. *capillaceus*
(Thuill.), var. *trisectus* Spenner, Fl. Frib. 4: 1008
(1829), nom. invalid.

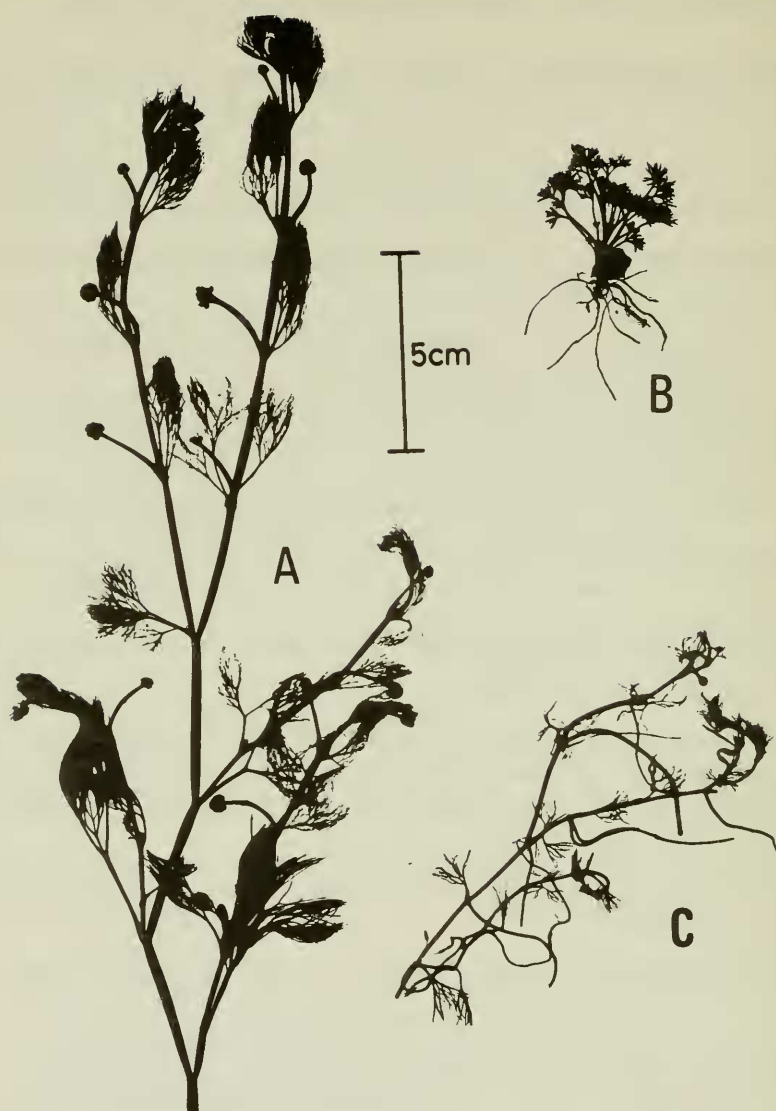


Fig. 19.: A & B) *R. trichophyllus* subsp. *trichophyllus* (A - aquatic state, B - terrestrial state); C) *R. trichophyllus* subsp. *lutulentus* (aquatic state).

B. rigidum (Persoon) F. Schultz, Arch. Fl. Fr. & Allem. 71
(1844).

Icones

Ibid fig. 19 A & 19 B.

Typification and Nomenclature

There can be few plant names that have received as much attention as *R. trichophyllum* Chaix. WILLIAMS, for example, managed to fill eighteen pages of the Journal of Botany (1908) on the nomenclature of this species, but it was not until 1952 that any authentic specimen was found.

The majority of authors who preferred more recent names to *R. trichophyllum* based their arguments on the assumption that CHAIX'S species was a nomen nudum. CHAIX'S prologue is as follows "trichophyllum (mihi) Hall. 1162: in rivulis limpidus, Valgaud. Devolny." CHAIX gave no diagnosis but there is a reference to "Hall. 1162" which is HALLER, Historia Stirpium Indigneram Helvetiae Inchoata, 2: 69, No. 1162 (1768). HALLER'S description is as follows:

" 1162. RANUNCULUS caule fluitante,
petiolis uniflorus, foliis capillaribus, laciniis divergentibus.

Foeniculum aquaticum, tertium TABERNAEMONT. p. 71.

Ranunculus trichophyllum, aquaticus, medio lutens

COLUMN. ecphras. p. 315.

Ranunculus aquaticus, albus, Foeniculi folio BARRELIER.
ic. 566.

Frequentissimus in rivulis quietis, fossique aqua
plenis. A. priori 1161 differt flore minori, foliis nulla quidem
certa figura circumscriptis, multo tamen brevioribus, divergen-
tibus. Flos. similis: tuba maxima

β. Foeniculum aquaticum, cornutum C. B. Prodr. p. 73.

J. B. Ill. p. 784.

Ranunculus aquaticus, albus, circinnatus, tenuissime diver-
sis foliis, floribus ex alis longis pediculis innixis PLUKNET.
p. 311. t. 55. f. 2.

Cira Nidan, Erlach, Mathod, in fossis quietis. J. B.
Genevae, C. B. in stagnis prope Hittelingen.

Prior proximus, folia habet a caule parum receden-
tia, omnino circulari circumscriptione terminata, lobis densissi-
me congestia, imbricatis. Nolui tamen a 1162 separare."

Although the following interpretation of HALLER'S description has appeared in print (DREW, *Rhodora* 38: 22 (1936)) I feel that, for the sake of completeness, it is worth quoting in full: - "CHAIX did not definitely state that, although HALLER'S No. 1162 included a variety β , he was referring to the " α " variety. Only by inference can it be established that CHAIX was referring to the latter under No. 1162, since a reference to a given plant which has one or more varieties is customarily interpreted as applying to the first element."

HALLER'S var β refers to *Ranunculus circinatus* Sibth., because the reference to PLUKENET'S plate is also cited by SIBTHORP (*Fl. Oxon.* 176, No. 503 (1794) in the original description of *R. circinatus*. Thus, CHAIX actually referred to two quite different species. However, it is possible to establish the identity of HALLER'S var. " α ", since he cites as synonymous *Ranunculus trichophyllum aquaticum medio luteus*. COL. Ecphr. 315, + 316 which, in turn, was listed by LINNAEUS under his var. γ .

DREW was concerned with the taxonomy of the North American species and was hindered by not knowing how many species in Europe could be included within HALLER'S description or more precisely within *Ranunculus aquatilis* L. var. γ . He was also unaware of any authentic specimens.

A. LOURTEIG (1951) while working on *Ranunculus* in South America, found a specimen in the herbarium of HALLER filius at Genève (G). This herbarium is generally considered representative of his father's collections and many of the plants were certainly collected by his father. I have not seen the specimen but have examined a photograph of it. It is in a terrestrial state but is fortunately in flower and fruit. The size and shape of the petals and the length of the pedicels in fruit (well shown in the photograph) leave little doubt that this specimen is the plant generally known as *Ranunculus trichophyllum*. Unfortunately, LOURTEIG interpreted the South American batrachian *Ranunculus* incorrectly and it is referable to *R. aquatilis*.

This specimen in the herbarium of HALLER filius cannot be designated holotype as there is no evidence that this was the specimen used by HALLER to write his diagnosis. There is, in fact, some contrary evidence. HALLER wrote "caule fluitante" in his diagnosis which could hardly refer to a specimen in a terrestrial state. As this is the only specimen found that could be

connected with HALLER I propose to designate it a neotype. A photograph of the type appears in LOURTEIG (1951).

Description

Annual or perennial, caespitose in terrestrial state or spreading-erect under water. Leaves divided into capillary segments, entire leaves absent; stipules oblong to ovate, adnate to petiole for $\frac{2}{3}$ or more their length; petiole up to 40 mm long; lamina globose to obconical; segments rigid or flaccid, divergent. Peduncles in fruit 11 - 48 mm long. Sepals 2.5 - 3.5 mm long, spreading, caducous. Petals 3.5 - 5.5 mm long, ovate to obovate, not contiguous during anthesis; nectar-pits lunate. Stamens 9 - 15. Carpels 16 - 33, hairy when immature, occasionally glabrous when mature; style subterminal. Receptacle hairy, remaining globose in fruit.

Distribution

R. trichophyllus is the most commonly collected and, perhaps, the most widely distributed species. It occurs throughout Europe except in the extreme north, North Asia, The Himalayas, North and West China, Japan, South East Australia, Tasmania and Central North America. Figure 20 is an outline map of the distribution of *R. trichophyllus* subsp. *trichophyllus*.

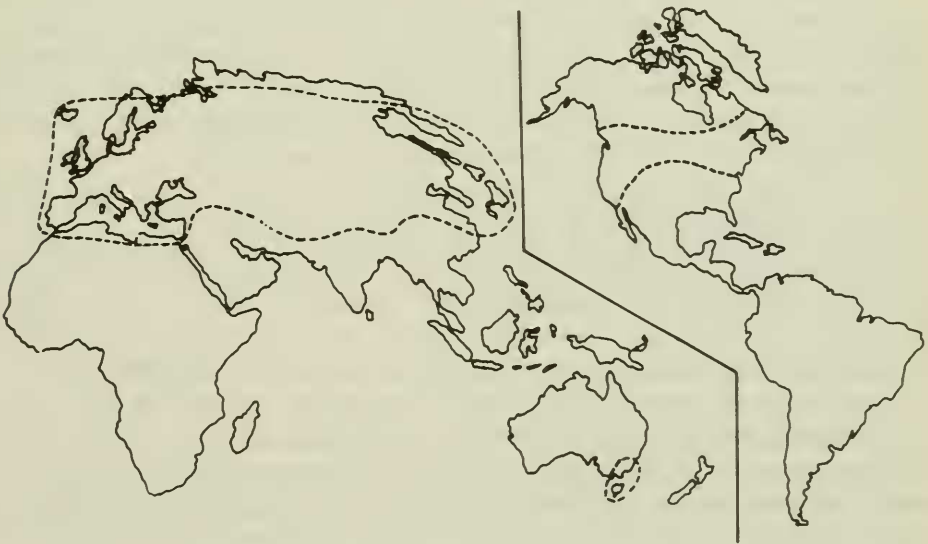


Fig. 20.: The distribution of *R. trichophyllus* subsp. *trichophyllus*.

Ecology

My field experience of *R. peltatus*, *R. aquatilis* and *R. trichophyllus* is confined to Europe but personal communications from L. BENSON about *R. aquatilis* and *R. trichophyllus* in North America and B. BRIGGS about *R. trichophyllus* in Australia suggest that the behaviour of these species is essentially the same in North America and Australia as in Europe.

R. peltatus, *R. aquatilis* and *R. trichophyllus* are normally found in temporary or disturbed aquatic habitats such as ponds, drainage ditches, newly dug pits, slowly flowing canals, small streams and artificially maintained fish pools. They are rarely found in water more than 1 m deep and will not tolerate deep shade or very swiftly flowing water. These species are characteristic pioneer plants of newly dug or recently cleaned pools and ditches. As the water matures, they are replaced by aquatic rhizomatous species such as *Potamogeton natans*, *P. crispus*, *P. pectinatus*, *Hippuris vulgaris*, *Nymphaea alba* or *Nuphar lutea* or by emergent reed swamp species such as *Typha latifolia*, *T. angustifolia*, *Sparganium erectum*, *Schoenoplectus lacustris*, *Glyceria maxima* or *Phragmites communis*.

R. trichophyllus is found in both eutrophic and oligotrophic waters but is more frequently found in eutrophic conditions. *R. peltatus* and *R. aquatilis* are confined to eutrophic waters but I have never found them sharing a habitat. *R. trichophyllus*, on the other hand, is frequently found growing intermingled with *R. aquatilis* or *R. peltatus*.

In permanent standing or flowing water they may persist as perennials as long as they are not smothered by larger or more robust species. In pools that dry out in summer they persist as terrestrial plants until late summer or early autumn if the substratum remains wet, and may persist as perennials if the habitat refills with water by early autumn. In pools that dry out completely every summer, they behave as winter or spring annuals. Seeds germinate in wet conditions at almost any time of the year, but seedlings only persist in winter if they are submerged in water as terrestrial plants are killed by frost. Submerged plants may be frozen in ice for several months without being killed.

In temperate latitudes flowering starts in late spring or

early summer and ceases during late summer or autumn. In tropical latitudes in the Andes of South America, LOURTEIG (1951, 1956) reports plants of *R. aquatilis* in flower during February, April, May, June, August, October and December.

R. peltatus, *R. aquatilis* and *R. trichophyllus* exhibit similar phenotypic and genotypic variation patterns. I believe this is due to genuine homologous variation and indicates close patristic affinities. When they are in a submerged or terrestrial, vegetative, divided-leaved state they are morphologically indistinguishable.

The following characteristics common to these species have been found to remain constant under different conditions in cultivation.

1. Petal number. The usual petal number is 5 but one population of *R. peltatus* (Pl-7) has from 8 - 14 petals. This plant has been self-pollinated and all offspring had supernumary petals.

2. Achene hairs. The immature achenes are hairy in all three species but the mature achenes may be densely hairy, nearly or completely glabrous or somewhat intermediate. The hairs on the achenes appear to be of two types, one with a basal constriction and the other without. The basal constriction is not a distinct feature and many hairs are intermediate and not easily assignable to either category. In plants with almost glabrous mature achenes the hairs have basal constrictions and as the achene matures, the hairs break off. The plants with hairy mature achenes bear hairs lacking basal constrictions. The intermediate plants bear a mixture of the two types of hairs. The following plants were found to belong to the three categories: a) persistent hairs: - Pl-1, Pl-2, Pl-4, Pl-5, Pl-7, A-2, A-3, A-6, A-7, A-8, A-9, A-10, A-11, Tt-1, Tt-4, Tt-6, Tt-7, Tt-10; b) intermediate: - Pl-8, A-4, A-5, Tt-2, Tt-5, Tt-8, Tt-9; c) caducous hairs: - Pl-3, Pl-6, Pl-9, A-12, Tt-3.

The plants Pl-3, Pl-4, Pl-6, Pl-7, Pl-8, Pl-9, A-3, A-6, A-12, Tt-1, Tt-2, Tt-3, Tt-7, Tt-8, Tt-9 have all been self-pollinated and in all cases the progeny resembled the parent and no segregation was detected. The following hybrids between hairy and intermediate plants of *R. trichophyllus* have been raised (female parent written first) Tt-1 x Tt-2 and Tt-2 x Tt-1. The F1 progeny were intermediate and when self-pollinated yielded inter-

mediate F2 progeny, but some segregation was detected as some of the intermediates were more hairy than others but no clear-cut ratios were seen and it is concluded that the inheritance of the different types of hair and the relative abundance of each of them is controlled by more than one pair of alleles. The cross Tt-1 x Tt-3 was attempted five times but the hybrids were inviable.

3. Peduncle length. When mature plants cultivated in shallow water are submerged in deeper water, the peduncles in some plants respond by elongating while in others they remain unchanged. The amount of elongation differs from plant to plant. The following plants remain unchanged or elongate only slightly when submerged: - Pl-4, Pl-5, Pl-7, A-1, A-2, A-3, A-4, A-6, A-8, A-9, A-12, Tt-1, Tt-4, Tt-7, Tt-9. The progeny from the hybrids Tt-1 (non-elongating) x Tt-2 (elongating) and Tt-2 x Tt-1 all had non-elongating petioles.

4. Rigid or flaccid divided leaves. The submerged divided leaves of most plants remain rigid and spreading when removed from water. The following plants have leaves that remain flaccid when removed from water: A-5, Tt-3, Tt-5, Tt-8. There appears to be some genetic basis for this characteristic but its expression is largely under environmental control and is discussed on page 71.

5. Annual or perennial habit. When plants are cultivated side by side under more or less uniform conditions in 25 cm of water and left undisturbed most of them are perennial but some show a tendency to be annual. The following plants show a tendency to be annual: Pl-3, Pl-6, Pl-9, Tt-6, Tt-7, Tt-9. If these plants are regularly pruned or cultivated in deeper water they become perennial.

None of the five characteristics listed above seem to be genetically linked to each other in any way but there is certain evidence that they are of selective advantage in some ecological situations. The only plants of *R. trichophyllus* collected from permanently flowing water (Tt-3, Tt-5, Tt-7) were also the only plants of this species with flaccid leaves. When rigid-leaved strains are cultivated in flowing water, they accumulate much debris on the leaves and show poor growth. All the plants showing a tendency to the annual habit were collected from the southern part of Europe where their habitat is more likely to dry out in summer; all the northern plants were perennial. It is worth noting

that the southern European and Oriental species *R. saniculi-folius*, *R. rionii* and *R. sphaerospermus* are obligate annuals. One would expect the achene hair characteristic to have some selective value in some situations as hairy achenes float much longer than glabrous ones, but I have been unable to correlate achene hairiness with any habitat factors.

R. trichophyllus lacks the potentiality for developing entire leaves; *R. peltatus* and *R. aquatilis* possess this potentiality, but under some conditions (see page 65) entire leaves do not develop. I have not discovered any strain of *R. aquatilis* or *R. peltatus* that never develops entire leaves but some plants, A-10 and A-11, for example, rarely produce entire leaves in their natural habitats in Bavaria, but develop them when cultivated in München Botanic Garden. In these examples, the plants in the wild were competing with other species, A-10 with *Potamogeton zizii* Roth. and A-11 with *Potamogeton pectinatus* L. and looked weak, but when transferred to the gardens and cultivated without competitors they became much more robust and developed entire leaves.

The diagnostic features of these three species (carpel and stamen number, petal-, sepal- and peduncle-lengths and petal, nectar-pit and leaf shapes) are discussed in the section on the evaluation of taxonomic characters. All these features are modified by environmental conditions and when plants are grown under poor conditions, such as low light intensity, low temperature or low nutrient level, *R. peltatus* tends to resemble *R. aquatilis* and *R. aquatilis* tends to resemble *R. trichophyllus*. Occasionally, however, I have been mistaken: for example, *R. aquatilis* (A-11) when first collected in the wild was thought by me to be *R. trichophyllus*, similarly *R. peltatus* (Pl-7) was originally collected as *R. aquatilis*. I have found that the best technique for positive identification is to cultivate the plant for a month or more and see if it changes its characteristics. From my cultivation work I am convinced this complex contains only three species.

- 12 a. Ranunculus trichophyllus Chaix subsp. lutulentus (Perrier
(Songeon) Vierhapper, Abhand. Zool.-Bot. Ges. Wien
16: 109 (1935).
- R. aquatilis L. var. eradicatus Laest., Nova Acta Reg.
Soc. Scient. Ups. 11: 242 (1839).
- Batrachium eradicatum (Laest.) Fr., Bot. Notiser 114 -
(1843).
- B. confervoides Fr., Bot. Notiser 121 (1845).
- R. confervoides (Fr.) Fr., Summa Veg. Scand. 139 (1846).
- R. paucistamineus Tausch. var. borealis Beurl., Bot.
Notiser 156 (1852).
- R. lutulentus Perrier & Songeon in Billot, Annot. Fl. Fr.
& Allem. 181 (1859).
- B. admixtum Nyl. in Nyl. & Sael., Herb. Mus. Fenn.
35 (1859).
- R. aquatilis L. var. sajanensis E. Regel, Bull. Soc. Nat.
Moscou 34: 39 (1861).
- R. capillus-naidis Arv. -Touv., Essai Pl. Dauph. 18
(1871).
- R. hydrocharis Spenner "form" confervoides (Fr.) Hiern,
J. Bot. Lond. 9: 102 (1871).
- R. aquatilis L. var. confervoides (Fr.) Lawson, Trans.
Roy. Soc. Canada 2: sect. 4, 45 (1884).
- B. paucistamineum (Tausch) F. Schultz var. eradicatum
(Laest.) Gelert, Bot. Tidsskr. 19: 27 (1894).
- R. trichophyllus Chaix var. confervoides (Fr.) Rikli in
Schinz & Keller, Fl. Schweiz 193 (1900).
- R. divaricatus Schrank var. eradicatus (Laest.) F. N.
Williams, J. Bot. Lond. 46: 21 (1908).
- R. flaccidus Persoon var. confervoides (Fr.) Hegi, Ill.
Fl. Mitteleur. 3: 585 (1912).
- R. trichophyllus Chaix var. eradicatus (Laest.) W. B.
Drew, Rhodora 38: 33 (1936).

R. codyanus Boivin, *Canad. Field Nat.* 63: 3 (1951).

B. trichophyllum (Chaix) F. Schultz subsp. *lutulentum*
(Perrier & Sonjeon) Janchen, *Cat. Fl. Austr.* 2:
196 (1958).

Icons

Ibid fig. 19 C.

Typification

I have seen two syntypes at Kew (K), one in flower (16 September) and one in fruit (2 October) "L' Aut-du-Pre, Mt. Mirantin, Savoie. PERRIER (1857)."

Description

Annual or perennial, terrestrial state caespitose, aquatic state prostrate with adventitious roots at almost every node. Leaves divided into capillary segments, entire leaves absent; stipules oblong to ovate, adnate to petiole for 2/3 or more their length; petiole up to 1.5 mm long; lamina obconical to subglobose; segments extremely fine, flaccid, sparsely branched. Peduncle in fruit 20 - 30 mm long. Flowers usually cleistogamous. Sepals 2 - 3 mm long. Petals 3 - 4.5 mm long, ovate to slightly obovate, not contiguous when flower opens; nectar-pits lunate. Stamens 9 - 13. Carpels 15 - 25, sparsely hairy when immature, often glabrous when mature; style subterminal. Receptacle hairy, remaining globose in fruit.

Distribution

R. trichophyllum subsp. *lutulentus* is an arctic-alpine found scattered throughout the Northern Hemisphere (fig. 21).

Ecology

R. trichophyllum subsp. *lutulentus* is an arctic-alpine. I have studied it in the Bavarian Alps and LUTHER (1951) has described its ecology in Finland. It is cleistogamous and frequently flowers and fruits completely submerged in water. At Funtensee, Berchtesgadener Alpen, I observed it in flower on 17 July 1960, 2.5 m below the water surface and in the same

the wild as living plants and Tl-3 was raised from seed. Plant Tl-3 has been self-pollinated and the progeny raised through three seed generations, all these plants have retained their parental characteristics. However, one plant (Tt-10), collected near Martigny-Ville in Switzerland that resembled subspecies *lutulentus* but reverted to subspecies *trichophyllus* in cultivation. If subspecies *trichophyllus* is cultivated in water between 6° and 8° C, it becomes delicate, procumbent, roots at most nodes and is generally indistinguishable from subspecies *lutulentus*. This situation, where different genotypes may have the same phenotype, is an interesting phenomenon from an evolutionary point of view, but is somewhat confusing to the taxonomist.

The arctic and alpine components of this subspecies are usually given different names but after comparative herbarium studies and cultivation experiments, I find this unjustifiable.

13. Ranunculus rionii Lager, Flora (Regensb.) 31: 49 (1848).
R. flaccidus Pers., var. parviflorum C. A. Meyer, Beitr. Pfl. Russ. Reich. 7: 55 (1849).
Batrachium rionii (Lager) Nyman, Bot. Notiser 98 (1852).
R. sedunensis Rion ex Wolf, Bull. Soc. Murith. 7 - 8: 28 (1879), fide Index Kewensis.
R. trichophyllus Chaix var. rionii (Lager) Rikli in Schinz & Keller, Fl. Schweiz 193 (1900).
R. flaccidus Pers. var. rionii (Lager) Hegi, Ill. Fl. Mitteleur. 3: 585 (1912).
R. trichophyllus Chaix subsp. rionii (Lager) Soó, A. Magyar Növ. Kezikönyve 222 (1951).
B. trichophyllum subsp. rionii (Lager) C. D. K. Cook, Mitt. Bot. München 3: 601 (1960).

Typification

I have seen an isotype at Kew (K) "In stagnis quibusdam circa Sedunum (Sitten) LAGGER."

Description

Annual, caespitose in terrestrial state, spreading-erect under water. Leaves divided into capillary segments, entire leaves absent; stipules ovate to suborbicular, adnate to petiole for more or less $\frac{2}{3}$ their length; petiole up to 20 mm long; lamina globoid; segments semi-rigid, divergent. Peduncles in fruit 30 - 50 mm long. Sepals 2 - 2.5 mm long, spreading. Petals 3.5 - 5 mm long, ovate to obovate, not contiguous during anthesis; nectar-pits lunate. Stamens 10 - 25. Carpels 60 - 90, less than 1 mm long, more or less globose, glabrous or slightly hairy at base of style; style lateral to subterminal. Receptacle hairy, elongating in fruit.

Distribution

R. rionii occurs in Europe in Austria, Czechoslovakia, Hungary and the Balkan peninsula. It is widely distributed in Asia and is found in Turkey, Syria, Lebanon, Georgia, Armenia, Iraq, Iran, Baluchistan, Afghanistan, Tibet, West and North China, Korea and Japan. It also occurs locally in South Africa and DREW (1936) mentions a plant of Western North America whose description fits that of *R. rionii* but as it was known from only one location DREW treated it as a monstrosity.

R. rionii was first described from Sion in the Vallais district of Switzerland in 1848. GAMS (1927) recorded it in his phytosociological description of the area from Follatères to Dent de Morcles and BECHERER (1956) lists it in his floristic study of the Vallais but from a personal communication he states that he has never seen it himself in nature. In 1961 I visited the Vallais of Switzerland and found abundant *R. trichophyllus* but no *R. rionii*. I have not seen any herbarium material of this species from Switzerland other than the type collection. I believe this species was an adventive in Switzerland that has now become extinct. From the overall geographical distribution of *R. rionii* it seems likely it has also been introduced into South Africa and North America. COOK and PATZAK (1962) describe the rediscovery and distribution of *R. rionii* in Austria. It is worth noting that *R. sphaerospermus* throughout its range is sympatric with *R. rionii* and that except in South Africa *R. rionii* is sympatric with *R. trichophyllus*. Figure 22 shows the distribution of *R. rionii* in the Old World.



Fig. 22.: The distribution of *R. rionii*.

Ecology

R. rionii is an annual that is usually found in pools that completely or partially dry out each summer. The flowering time (determined from herbarium specimens) is from June to August in Europe, January to July in Asia Minor, March to July in Tibet and August to March in South Africa.

Variation

Except for its well defined floral characteristics *R. rionii* is indistinguishable from *R. trichophyllus* and exhibits the same phenotypic variation patterns in cultivation.

14. Ranunculus circinatus Sibth., Fl. Oxon. 175 (1794).

R. aquatilis L. B. millefolius Miljeblad, Sw. Fl. 229
(1792), fide Hiern (1871).

R. aquatilis L. var. circinatus (Sibth.) With., Arr. Brit.
Pl. ed. 3, 2: 507 (1796).

R. aquatilis L. var. orbiculatus Schum., Enum. Pl. Saell.
171 (1801).

Batrachium caespitosum sensu S. F. Gray, Nat. Arr. Brit.
Pl. 2: 722 (1821), non Thuill.

R. stagnatilis Wallroth, Sched. Crit. 285 (1822).

R. aquatilis L. var. stagnatilis (Wallroth) DC., Prodr.
1: 27 (1824).

R. hydrocharis B. homoiophyllus var. stagnatilis (Wallroth)
Spenner, Fl. Frib. 4: 1009 (1829), nom. invalid.

B. circinatum (Sibth.) Spach, Hist. Veg. (Phan.) 7: 201
(1839), nom. legit.

R. hydrocharis Spenner "form" circinatus (Sibth.) Hiern,
J. Bot. Lond. 9: 99 (1871), nom. invalid.

B. foeniculaceum (Gilib.) Krecz. in Komarov. Fl. URSS.
7: 338 (1937), nom. invalid.

Icons

Plukenet, L., Almagestum Botanicum t. 55, fig. 2 (1696).

Glück, H. Wasser- und Sumpfgewächse, 4: t. 1, fig. 5 - 11 (1924).

Typification & Nomenclature

In his original description SIBTHORP cited *R. aquatilis* L. var. γ , as a synonym of *R. circinatus*. WILLIAMS (1908) pointed out that the " γ " is a typographical error for " β " as SIBTHORP refers to PLUKENET'S diagnosis and plate in *Almagestum Botanicum* 331, t. 55, fig. 2 (1696) which is the basis of LINNAEUS'S var. β .

SIBTHORP cited "Christ Church Meadow, South Leigh" as a locality for this species. No authentic specimen has been found so rather than choose a neotype for this distinct species I designate

PLUKENET'S plate as a typotype (DANDY in STEARN 1957).

The earlier name *R. divaricatus* Schrank has occasionally been adopted for this species instead of *R. circinatus*. This is not justified as SCHRANK, Baier. Fl. 2: 104 (1789), after an inconclusive diagnosis, cited HALLER No. 1162, the "♂" element of which is the type of the earlier species *R. trichophyllus* (see p.132) so the name *R. divaricatus* was illegitimate at publication. SCHRANK also cited a plate of TABERNAEMON-TANUS, Neuw. Kreuterb. 187 (1664) which is a poor illustration that could be *R. trichophyllus* but is certainly not *R. circinatus*.

Description

Long-lived perennial or occasionally annual; stems 5 - 300 cm. Leaves divided into capillary segments, entire leaves absent; stipules ovate, adnate to petiole for 3/4 or more their length, apex obtuse; petiole 2 - 5 (10) mm long; lamina circular to semi-circular; segments rigid, divergent, lying in one plane. Peduncles in fruit 20 - 100 mm long. Sepals rarely exceeding 6 mm long, spreading. Petals rarely exceeding 10 mm long, obovate, contiguous during anthesis; nectar-pits lunate. Stamens (5) 20 - 24 (27). Carpels (30) 42 - 48 (56), hairy when immature, occasionally glabrous when mature; style lateral. Receptacle hairy.

Distribution

R. circinatus occurs in North West and Central Europe and Central North Asia (fig. 16). It has been recorded from North America (GRAY 1895, MUENSCHER 1944) but these records are almost certainly based on misidentifications of *R. longirostris*.

Ecology

R. circinatus is normally a long-lived perennial but SALISBURY (1960) suggests that it may occasionally behave as an annual. It is found in areas of permanent water in lakes, gravel pits and slowly flowing rivers and canals. It is usually found in eutrophic waters but is occasionally found in oligotrophic conditions. OLSEN (1950) has recorded it in brackish water and classifies it as Infra-Mesohalobous tolerating salinities up to 18%.

R. circinatus is probably the most hydatophytic species in *Ranunculus* and is normally found in water between 1 and

3 m deep. LUTHER (1951) records it in 5 m in Finland. It has very little resistance to desiccation and can be grown terrestrially only in moist conditions with long photoperiods. Terrestrially cultivated plants grow very slowly and do not flower.

Throughout its geographical range the flowering time is from May to August but flowering is very erratic and populations may not flower every year. LUTHER (1951) reports that it rarely flowers and fruits in Finland and that it is effectively spread by human agencies, fragments often being found attached to boats.

Variation

No genotypic variation causing morphological differences has been detected. There are occasionally differences in fertility between different populations but this is probably an environmental effect as it is usually the less vigorous plants that exhibit the highest sterility.

Although there is rarely any difficulty in recognising this species, it shows a remarkable degree of phenotypic variation. For example, under different cultivation conditions the internode length varied from 1 - 20 cm, the peduncle from 2 - 10 cm and the number of ultimate leaf segments from 5 - 160. GLÜCK (1924) recognised and described six formae (*typicus*, *parviflorus*, *globuliformis*, *elongatus*, *capillaceus* and *terrestris*). These formae are based on more or less arbitrarily chosen characteristics such as internode length, flower diameter and number of ultimate leaf segments. Each of GLÜCK'S formae has been seen by me, on ramets of a single clone in cultivation. GLÜCK'S tables and illustrations (p. 136 - 146) give a good overall indication of the plasticity of this species. However, the plastic responses in this species are very complicated and the previous conditioning is important.

R. circinatus exhibits two distinct growth states, one prostrate and branching, the other erect and simple. In nature, the prostrate state is usually found during the winter but may persist throughout the summer particularly if the plants are subjected to shade or swiftly flowing water. In cultivation the prostrate state is readily induced if the plants are put in poor conditions such as low light intensity, cloudy water or low nutritional level. In the prostrate state roots develop at most nodes and the stems grow along the substratum. If a plant in the prostrate state is

lifted above the substratum the stems will grow downwards for 1 m or more and detached portions sink. During the prostrate phase the internodes are short (1 - 3 cm), the leaves somewhat irregular and no flowers are produced.

The erect state develops during the summer. The stems usually grow up to the surface of the water and rarely develop roots at the nodes, detached portions float to the surface; the internodes are very variable in length. Flowering often starts 25 cm or more below the water surface and when this happens the peduncles tend to be very long (up to 10 cm) and the flowers tend to be cleistogamous. Both erect and prostrate states can exist at the same time on the same individual.

15. Ranunculus longirostris Godron, Mém. Soc. Roy. Nancy 1839: 39 (1840).

R. circinatus Auct. Amer.

R. aquatilis L. var. *stagnatilis* sensu Hooker, Fl. Bor. - Amer. 1: 10 (1829) non Wallroth, nec DC.

Batrachium longirostre (Godron) F. Schultz, Arch. Fl. Fr. & Allem. 71 (1844), nom. legit.

R. hydrocharis Spenner "form" *longirostris* (Godron) Hiern, J. Bot. Lond. 9: 100 (1871), nom. invalid.

R. aquatilis L. var. *longirostris* (Godron) Lawson, Trans. Roy. Soc. Canada sect. 4, 2: 45 (1884).

R. usneoides Greene, Leaflets Bot. Obs. & Crit. 2: 106 (1910).

Icones

Godron, G. Essai sur les renoncules a fruits ridés transversalement, Mém. Soc. Roy. Nancy 1839: fig. 9 (1840).

Typification

Holotype in Paris (P) "Eaux courantes, St. Louis, Missouri, Juin 1838, No. 52, N. RIEHL" seen by BENSON (1954). I have seen an isotype at Kew (K).

Description

Perennial up to 100 cm tall. Leaves divided into capillary segments, entire leaves absent; stipules ovate to suborbicular, adnate to petiole for 1/2 or more their length; petiole up to 10 mm long; lamina globoid; segments fine, rigid, divergent. Peduncle in fruit 30 - 50 mm long. Sepals 3 - 4 mm long, spreading, frequently blue-tipped. Petals 4 - 9 mm long, broadly obovate, contiguous during anthesis; nectar-pits lunate. Stamens 10 - 20. Carpels 7 - 30, glabrous or hairy; style terminal, persistent in fruit, 0.7 - 1.1 mm long (at least 1/3 the length of the mature achene). Receptacle hairy, remaining globose in fruit.

Distribution

R. longirostris shows a continental distribution pattern in Central North America (fig. 23).



Fig. 23. : The distribution of *R. longirostris*.

Ecology & Variation

I have not seen living material of this species nor have I succeeded in finding a correspondent who is familiar with this species in the field. From herbarium studies *R. longirostris* appears to be the North American vicariant of *R. circinatus*.

16. Ranunculus fluitans Lam., Fl. Fr. ed. 2, 3: 184 (1778).

R. fluviatilis Wigg., Prim. Fl. Holsat. 42 (1780) non Bigel, nec Pursh.

R. aquatilis L. subsp. *peucedanifolius* Ehrh., Hanover. Mag. 1780, 15: 225 (1780).

R. peucedanifolius (Ehrh.) All., Fl. Pedem. 2: 53 (1785).

R. aquatilis L. var. *fluviatilis* (Wigg.) With., Arr. Brit. Pl. ed. 3, 2: 507 (1796).

? *R. peucedanoides* Desf., Fl. Atl. 1: 444 (1798).

Batrachium fluviatile (Wigg.) S. F. Gray, Nat. Arr. Brit. Pl. 2: 722 (1821).

B. peucedanifolium (Ehrh.) Dumort., Fl. Belg. 127 (1827).

B. fluitans (Lam.) Wimmer, Fl. Schles. 9 (1841), nom. legit.

B. pumilum (Poir.) Nyman, Bot. Notiser 98 (1852) is cited in Index Kewensis as a synonym of *R. fluitans* but this name does not appear in this reference, nor has it been traced.

Icones

Moss, C. E., Cambridge British Flora 3: t. 152 (1920).

Butcher, R. W., New Ill. British Flora 1: 313 (1961).

Ibid fig. 24.

Typification

The type specimen should be at Museum National d' Histoire Naturelle, Paris (P) but I have not seen it.

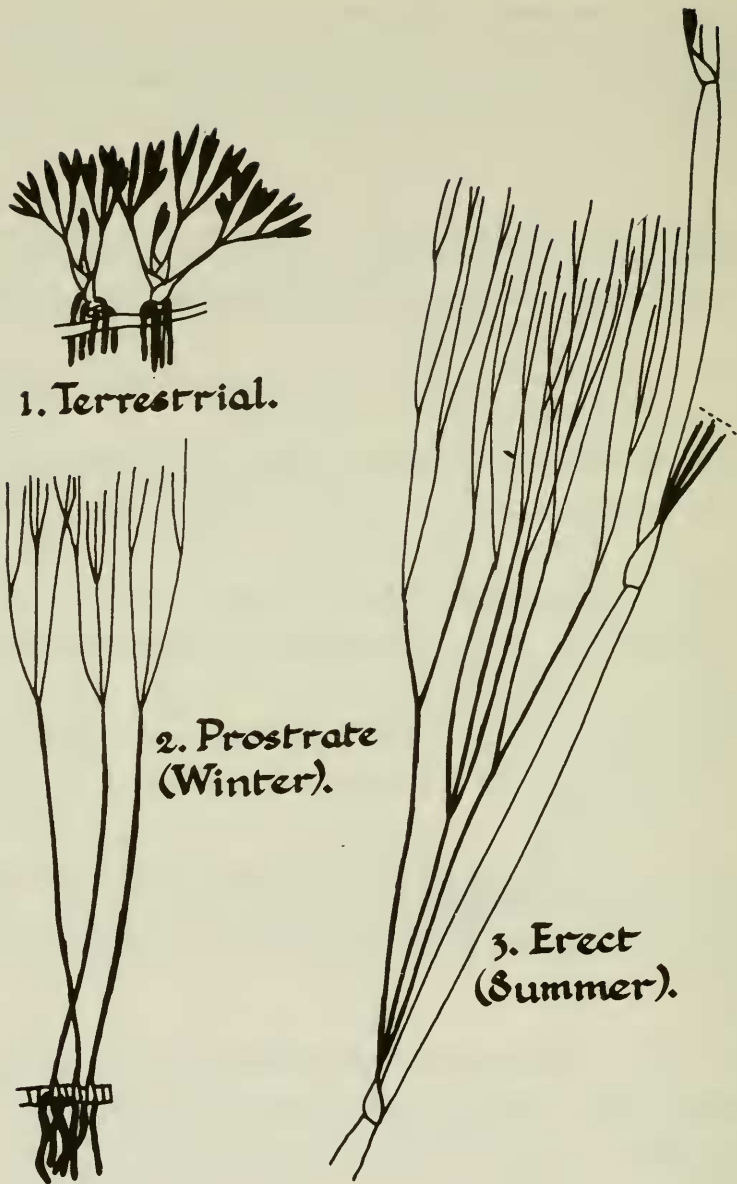


Fig. 24.: *R. fluitans*.

Description

Since this is a highly plastic species separate descriptions of the aquatic and terrestrial states are given.

The aquatic state:

Long-lived perennial; stem up to 6 m long, internodes up to 35 cm long. Leaves divided into capillary segments, rarely less than 8 cm long, entire leaves absent; stipules oblong to ovate, adnate to petiole for $\frac{3}{4}$ or more their length; petiole up to 22 cm long (usually long in winter and short in summer); lamina up to 25 cm long, elongate-obconical; segments few, very long, firm, sub-parallel, rarely more than 4 times forked. Peduncle in fruit 4 - 10 cm long. Sepals 4 - 6.5 mm long, spreading. Petals 5 - 10, 7 - 13 mm long, broadly obovate, contiguous during anthesis; nectar-pits elongate-ovate to pyriform. Stamens 20 - 35. Carpels 34 - 63, sparsely pubescent when immature, frequently glabrous when mature; style lateral. Receptacle glabrous or very nearly so.

The terrestrial state:

Annual, rarely exceeding 6 cm tall, internodes 0.5 - 10 mm long. Leaves divided into capillary segments, 15 - 45 mm long; segments rigid, sub-parallel, distinctly flattened, often apiculate at the tips. Flowers very rare, similar but smaller than aquatic state, almost invariably sterile.

Distribution

Local in West and Central Europe (fig. 25).

Ecology

R. fluitans is usually found in permanently flowing water but occasionally colonises almost stationary water in large drainage ditches where it rarely flowers. It requires a fairly stable substratum and is normally confined to larger rivers with pebble covered bottoms. In the Rivers Dove, Wye and Derwent in Derbyshire, England, *R. fluitans* is almost entirely confined to the non-limestone areas while in the same rivers in limestone areas, it is replaced by *R. penicillatus*. From transplant experiments in the River Wye and cultivation experiments in calcium-free and calcium-rich conditions, it appears that the physical nature of the substratum and not its calcium concentration is a limiting factor in distribution. Fragments of chalk and many limestones



Fig. 25. : The distribution of *R. fluitans*.

do not weather to smooth pebbles and remain unstable during periods of flooding while igneous and metamorphosed rocks usually weather to smooth pebbles, collect silt round themselves and remain stable during floods.

Further observations in the waterways surrounding München, Germany support this substratum-stability hypothesis. In the pebble-bottomed River Isar and Schleissheimer Kanal, one finds *R. fluitans*, while in the adjoining River Würm, an artificially maintained flood outlet for Starnberger See, one finds the sterile triploid hybrid *R. fluitans* X *trichophyllus* (thought to be the parent hybrid of the amphidiploid *R. penicillatus* var. *calcareus*).

R. fluitans, like *R. circinatus*, has two growth states: a summer, non-rooting, quick-growing, elongate, flowering state and an autumn to spring, rooting, slow-growing, prostrate, compact, non-flowering state (fig. 24). *R. penicillatus* and the hybrid *R. fluitans* X *trichophyllus* do not have these different states and are able to root and spread actively throughout the year. Individual plants of *R. fluitans* have been watched for three years (1957-1959) at Quorndon, Derbyshire and Temple Bridge, Suffolk, and each individual plant has retained almost the same shape and size without any change in position. During the same period in the River Wye, Derbyshire, individual plants of *R. fluitans* X *aquatilis* (or *trichophyllus*) at Monsal Dale and *R. penicillatus* var. *calcareus* at Haddon all moved and changed shape, some cushions disappeared while others split into two or more. These observations tend to indicate that the mode of growth limits the spread of the plants on different substrata.

In *R. fluitans* the prostrate state gives way to the elongate state in April or May. Once the elongate state has been formed, growth is extremely fast and stems 3 m long may be achieved in 3 months. These long stems are somewhat fistulose and very buoyant. In August and September or during the summer if the water level drops sufficiently low these long stems become detached and float downstream. Excessive growth of *R. fluitans* or the accumulation of detached stems may constitute a hazard to waterways. In many waterways *R. fluitans* is controlled by regular cutting or periodically dropping the water level.

The flowering time is from June to August but it does not

flower every year. This species is fairly tolerant of pollution as long as the water remains clear but will not flower in polluted water. If, however, the water becomes cloudy or shaded, it soon dies. *R. fluitans* has become extinct or rare in many of the larger rivers in the Midland region of England.

Variation

R. fluitans is a difficult plant to work with in cultivation as it requires a great amount of space and flowing water before it reaches maturity. I find that it grows well but remains in a vegetative state when cultivated in still water in tanks but GLÜCK (1924) has reported flowering in plants cultivated in still water.

In nature, in permanently flowing water, it is elongate in summer with long, fistulose internodes and short petioles (fig. 24) and in winter it is prostrate with very short, non-fistulose internodes and long petioles; roots are confined to prostrate parts of the stem. When cultivated in winter in a greenhouse maintained at approximately 10°C it remains semi-elongate with long, non-fistulose internodes and long petioles. When cultivated in summer in still water, prostrate, intermediate and elongate states may develop on different parts of the same plant or on different plants. The factors controlling the production of these states are not understood and it is not unusual to find ramets side by side in one tank in different states. The only generalisation it is possible to make is that if a plant is put in adverse conditions for growth, it reverts to the prostrate state.

Under a regime of long photoperiods *R. fluitans* can be cultivated terrestrially. The terrestrial state looks very different from any of the aquatic states. The whole plant forms a tight cushion with very short internodes, comparatively long petioles and short, flattened ultimate leaf segments (fig. 24).

GLÜCK (1924) recognised three varieties (*fluitans*, *latifolius* and *heterophyllus*). Variety *heterophyllus* is referable to *R. penicillatus*. Variety *latifolius* is described as differing from var. *fluitans* in possessing flattened ultimate leaf-segments in the aquatic state. GLÜCK records this character as remaining constant in cultivation in still water. I have not seen living material of this variety but I believe it may have a genetic basis as one plant (F-6. Donaueschingen, Germany) showed a tendency to slightly flattened segments when cultivated in still water at München during the summers of 1960 and 1961. In a

terrestrial state this plant developed very broad flattened leaf segments. Excluding var. *heterophyllus*, GLÜCK'S descriptions and tables (p. 176-186) give a good impression of the overall variation of this species.

B. bachii Wirtgen, Verh. Nat. Ver. Preus. Rheinl., 3: 8-10 (1846) (*R. fluitans* Lam. var. *bachii* (Wirtgen) Wirtgen, Fl. Preus. Rhpr. 15 (1857) is a very strange plant that GLÜCK (1924) thought to be a starved state of *R. fluitans*. Its leaves resemble *R. fluitans* and its flowers resemble *R. trichophyllus*. It is found in a few localities scattered throughout the range of *R. fluitans*. It is invariably sterile and I believe it is a hybrid between *R. fluitans* and *R. trichophyllus* but it does not resemble the hybrid plants NH-4 and NH-5 which I believe to have the same parent species. As both *R. trichophyllus* and *R. fluitans* are themselves genetically variable and exist at different polyploid levels it is possible for hybrids between them to show considerable variation.

17. *Ranunculus penicillatus* var. *penicillatus* (Dumort.) Bab., Man. Brit. Bot. ed. 7, 7 (1874).

R. fluitans var. *heterophyllus* Cosson & Germ., Fl. Env. Paris 1: 11 (1845).

R. aquatilis α *longifolius* Rossm., Beitr. Kennt. Wasserröhrenfüsse 58 (1854).

Batrachium penicillatum Dumort., Bull. Soc. Bot. Belg. 2: 216 (1863), nom. legit.

R. aquatilis L. var. *pseudofluitans* Syme in Sowerby, Engl. Bot. ed. 3, 1: 20 (1863).

R. pseudofluitans Newbould ex Syme, loc. cit., nom. synonym. (not validly published).

R. pseudofluitans (Syme) Newbould ex Baker & Foggitt, Thirsk Nat. Hist. Soc. Bot. Exch. Club, Cur. Rep. 1864: 5 (1865); J. Bot. Lond. 3: 115 (1865).

R. heterophyllus Weber subsp. *pseudofluitans* (Syme) Moore & More, Cybele Hibernica 5 (1866).

R. hydrocharis Spenner "form" *penicillatus* (Dumort.),
"form" *pseudofluitans* (Syme) Hiern, J. Bot. Lond.
9: 98 - 100 (1871).

R. kaufmanii Clerc, Zap. Ural. Obshch. Lyub. Estest. 4:
107 (1878).

? *R. vaginatus* Freyn in Willk. & Lange, Prod. Fl. Hisp.
3: 908 (1880).

R. cambricus A. Bennett ex Druce, Rep. Bot. Exch. Club
Brit. Isles 1892: 351 (1893).

R. fluitans proles *flabellifolius* Rouy & Fouc., Fl. Fr. 1:
72 (1893).

R. aquatilis subsp. *marizii* Cout., Fl. Port. 231 (1913).

B. pachycaulon Neviski, Acta Inst. Bot. Ac. Sci. URSS. ser. 3,
4: (1937), fide Krecz in Komarov, loc. cit.

Icons

Ibid fig. 26

Typification

The holotype is in the Herbarium of the Jardin Botanique de l'Etat, Bruxelles (BR). It is an adequate specimen collected from Flandre by SCHEIDWEILER. The herbarium sheet bears no date or collector's number but bears a label with *Batrachium penicillatum* Nob. written in DUMORTIER'S own handwriting.

This species has frequently been called *R. pseudofluitans* (Syme) Newbould ex Baker & Foggit but this is a later name at specific rank than *R. penicillatus* and must be rejected.

Description

Long-lived perennial, stem up to 3 m long in flowing water. Leaves entire or divided into capillary segments. Entire leaves alternate, frequently lacking; stipules suborbicular to ovate, adnate to petiole for $\frac{3}{4}$ or more their length; petiole 50 - 80 cm long; lamina up to 40 cm wide, reniform to semi-orbicular occasionally cuneate at base, 3- or 5-lobed; lobes cuneate, sinus $\frac{2}{3}$ or less the length of the lamina; margin entire, crenate, dentate or with capillary appendages. Divided leaves invariably present, alternate,



Fig. 26.: *R. penicillatus* var. *penicillatus*.

exceeding internodes on mature stems; petiole 5 - 30 mm long; lamina elongate-obconical, 7 - 20 cm long, segments numerous, flaccid, fine, sub-parallel. Peduncle in fruit 50 - 100 mm long, usually longer than the petiole of the opposed entire leaf. Sepals 3 - 7 mm long, spreading. Petals (5) 10 - 15 (20) mm long, broadly obovate, contiguous during anthesis; nectar-pits elongate, more or less pyriform. Stamens (8) 20 - 40. Carpels (15) 50 - 80, hairy or glabrous; style lateral to subterminal. Receptacle distinctly hairy, remaining globose in fruit.

Distribution, Ecology and Variation are described on page 160 .

17 a. Ranunculus penicillatus var. calcareus (R. W. Butcher) comb. nov.

R. calcareus R. W. Butcher, The Naturalist (Yorkshire)
1960: 125 (1960).

Icones

Butcher, R. W. & Strudwick, F. E., Further Ill. Brit. Pl. 15 (1930).

Butcher, R. W. New Ill. Brit. Fl. 1: 217 (1961).

Ibid fig. 27.

Typification

The holotype is in R. W. BUTCHER'S private Herbarium at Ghalene, Hellstone Close, Portesham, Weymouth, Dorset, England. It was collected from the River Lea, Hertfordshire, England by BUTCHER with collection number 4. I have not seen the holotype but have seen material from the locus classicus.

Diagnosis

Like var. *penicillatus* but divided leaves obconical in outline, equal to or shorter than mature internodes; segments rigid or flaccid, slightly divergent, much branched, with up to 150 ultimate segments.

Distribution, Ecology and Variation described on page 160 .



Fig. 27.: *R. penicillatus* var. *calcareus*.

17 b. Ranunculus penicillatus var. vertumnus var. nov.

Diagnosis

A var. *penicillato* foliis omnibus capillaribus dissectis, ambitu globosis usque reniformibus, internodiis maturis brevioribus; segmentis rigidis, patentissimis, multifidis, segmentis ultimis plus quam 200, differt.

Like var. *penicillatus* but lacks entire leaves; divided leaves globose to reniform, shorter than mature internodes; segments rigid, widely divergent, much branched, with more than 200 ultimate segments.

Typification

The holotype is deposited in the Herbarium at Kew (K). "In the Basingstoke Canal where it meets the River Greet, Greywell, about 8 km east of Basingstoke, Hamshire, England. coll. C. D. K. COOK, 18 May 1958."

The name *vertumnus* is derived from the latin verb *vertere* (to change). *Vertumnus* was the name of a Roman agricultural divinity who assumed several different guises in order to seduce Pomona. He was also venerated with the god of the River Tiber, the course of which he was supposed to have altered.

Icones

Ibid fig. 28.

Distribution

R. penicillatus sensu lato occurs throughout Europe except in the extreme north and the Balkan peninsular. Figure 29 shows the distribution of each variety as far as it is known at the moment. The total geographical distribution is poorly known and each dot represents one known locality.

Ecology

R. penicillatus sensu lato is found in flowing water in streams, small rivers and canals. Unlike *R. fluitans*, *R. penicillatus* does not form a prostrate state and is capable of developing roots from internodes throughout the year so it is able to maintain itself on unstable substrata.



Fig. 28. : *R. penicillatus* var. *vertumnus*.

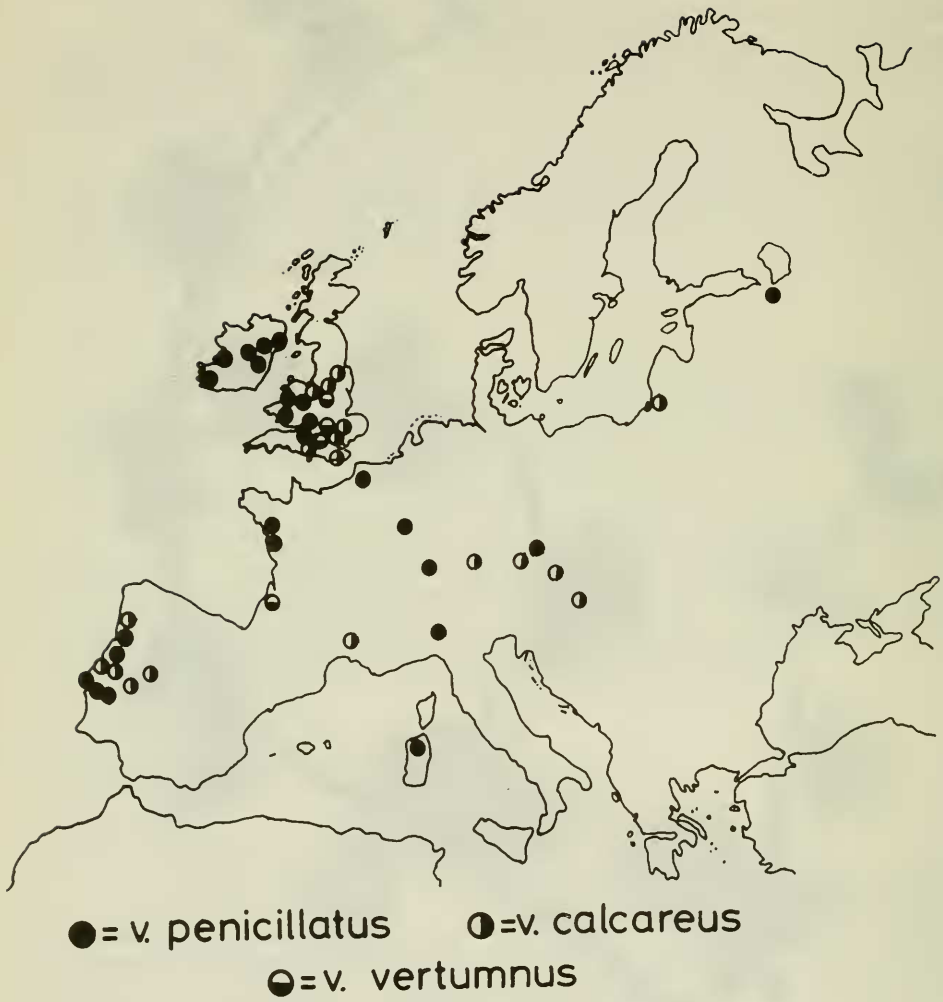


Fig. 29. : The distribution of *R. penicillatus*.

Var. *penicillatus* is found in very fast flowing water and may inhabit rapids or small waterfalls. Var. *calcareus* is found in streams and small rivers that are normally fairly slow-flowing but are subject to frequent flooding when the water may be very swift-flowing. Var. *vertumnus* is found in slow-flowing rivers and canals that have clear water and are not subject to frequent flooding.

Variation

The *R. penicillatus* group requires more study and is a long way from being understood. The treatment given here is conservative. In cultivation it is possible to recognise several different races but their phenotypic variation is so great that their detection in the herbarium and the field is impossible on gross morphological features. In the wild they are confined to flowing water. In cultivation they grow well in still water but some strains will not flower or develop entire leaves. The characters that are seen to differentiate the races in cultivation are length, number and diameter of leaf-segments, internode-length and rate of growth but these are the very characters that are most under environmental control.

The total variation pattern of *R. penicillatus* extends from strains that resemble *R. peltatus* to strains that superficially resemble *R. fluitans*. *R. penicillatus* may be separated from *R. fluitans* as it has a densely pubescent receptacle, does not form a prostrate state and has ovate to suborbicular stipules. At the other end of the variation spectrum, however, it is occasionally difficult to separate *R. penicillatus* from *R. peltatus*. In all strains the flower closely resembles that of *R. peltatus* but is larger and has more stamens and carpels. Unfortunately, flower size and the number of stamens and carpels are very much under environmental control (see page 77 and fig. 6) and the range of variation of *R. penicillatus* embraces that of *R. peltatus* so it is often impossible to distinguish these species on floral characteristics.

Fertility is also largely under environmental control and plants cultivated under poor conditions rarely develop any well-formed pollen grains or achenes so it is often difficult to distinguish the fertile amphidiploid *R. penicillatus* from the sterile hybrids that may have given rise to it. The evolution of *R. penicillatus* is described on page 203 & 216.

The Karyotype

Chromosome number

Ranunculus subgenus *Batrachium* has a basic chromosome number of 8, which according to KURITA (1958 a) is the commonest in *Ranunculus* and the *Ranunculaceae* as a whole. Within the *batrachia* there are diploids, triploids, tetraploids, pentaploids and hexaploids. No accessory or 'beta' chromosomes have been detected and apart from artificially synthesized hybrids no aneuploids have been found.

The following is a list of all the chromosome numbers reported for wild-collected plants of *Ranunculus* subgenus *Batrachium*. Only *R. lobbii*, *R. flavidus* and *R. longirostris* remain uncounted.

Species	Count	Origin and Voucher	Reported by
R. hederaceus	2n = 16	Origin and voucher unknown.	LANGLET (1927)
"	2n = 16	Kandestederne, Skagen, Denmark. Coll. T.W. BÖCHER, no voucher.	BÖCHER (1938)
"	2n = 16	Sellindge, Hythe, Kent, England. Coll. O.R. STAPLES, 1956, CGE..	COOK (1962)
"	2n = 16	Ponsongath, The Lizard, Cornwall, England. Coll. C.D.K. COOK, 1958. C, CGE, LIVU, M.	COOK (1962)
"	2n = 16	Mora, Alto Alentejo, Portugal. Coll. B. V. RAINHA, 1958. CGE.	COOK (1962)
"	2n = 16	Eifel, Wirftal, Stadtkyll, Prüm, Germany. Coll. D. PODLECH, 1961, C, CGE, M.	COOK (1962)
"	2n = 16	Bwlch-y-Rhiw, Aberdaron, Caernar- vonshire, Wales. Coll. C.D.K. COOK, 1962. LIVU.	COOK 1st report
"	2n = 16	Penrhos Lligwy, Anglesey, Wales. Coll. C.D.K. COOK, 1962. LIVU.	COOK 1st report
"	2n = 16	Porthmynawyd, Pembroke, Wales. Coll. J.J. GILL, 1964. LIVU.	COOK 1st report
R. hederaceus	2n = 32	Artificial autotetraploid induced from the Ponsongath plant, CGE, LIVU, M.	COOK (1962)

Species	Count	Origin and Voucher	Reported by
R. omiophyllus	2n = 16	Polizzi Generosa, Madonie Mts. Sicily. Coll. C.D.K. COOK, 1961. C, CGE, LIVU, M.	COOK (1962)
R. omiophyllus	2n = 32	Origin and voucher unknown.	LARTER (1932)
"	2n = 32	Abbots Moss, Marton, Cheshire, England. Coll. K. GOODWAY, 1959. LIVU.	COOK 1st report
"	2n = 32	Two Bridges, Dartmoor, Devon, England. Coll. C.D.K. COOK, 1958. C, CGE, M.	COOK (1962)
R. ololeucos	2n = 16	Maarn, Utrecht, Holland. Coll. C.D.K. COOK & T. W. K. GADELLA, 1960. CGE, M.	COOK (1962)
R. tripartitus	2n = 48	Kynance, The Lizard, Cornwall, England. Coll. C.D.K. COOK, 1957. C, CGE, M, LIVU.	COOK (1962)
"	2n = 48	Arne, Dorset, England. Coll. C.D.K. COOK, 1957, CGE.	COOK (1962)
"	2n = 48	Kynance, The Lizard, Cornwall, England. Coll. D.E. COOMBE, 1964. LIVU.	Cook 1st report
"	2n = 48	Arne, Dorset, England. Coll. E. M. BURROWS, 1964. LIVU.	COOK 1st report

R. baudotii	2n = 32	Origin and voucher unknown.	LANGLET (1927)
"	2n = 32	Saltholm in Øresund, Denmark. Coll. T. W. BÖCHER, no voucher.	BÖCHER (1938)
"	2n = 32	Aflandshage, Denmark. Coll. T. SØRENSEN, Sept. 1954. no voucher found.	CHRISTIANSEN in SØRENSEN (1955)
"	2n = 32	Brading, Isle of Wight, England. Coll. C. D. K. COOK, 1958. C, CGE, LIVU, M.	COOK (1962)
"	2n = 32	Zicksee, St. Andrat-Frauenkirchen S. E. Austria, Coll. C. D. K. COOK & A. PATZAK, 1960. C, CGE, LIVU, M.	COOK (1962)
"	2n = 32	Gennarbyviken, Tenala, Finland. Coll. H. LUTHER, 1961. LIVU.	COOK 1st report
R. saniculifolius	2n = 16	Prastio, Cyprus. Coll. D. MEIKLE, May 1962. No. 618. LIVU.	COOK 1st report
R. peltatus	2n = 16	Seed from Coimbra Bot. Gdn., Portu- gal. 1964. COOK. LIVU.	COOK 1st report
"	2n = 16	Sevilla, Spain. Coll. J. POELT, 1962. LIVU.	COOK 1st report
"	2n = 16	Casa Bravea, Portugal. Coll. J. POELT, 1964. LIVU.	COOK 1st report
R. peltatus	2n = 32	Hestehaven, Denmark. Coll. and counted K. LARSEN, 18 May 1952. C.	COOK (1962)

Species	Count	Origin and Voucher	Reported by
<i>R. peltatus</i>	2n = 32	Bastrup, Denmark. Coll. and counted K. LARSEN, 13 May 1953. C.	COOK (1962)
"	2n = 32	Plejelt, North of Fredensborg, Denmark. Coll. and counted K. LARSEN, 17 May 1953. C.	COOK (1962)
"	2n = 32	Baebakke, Fyns Hoved, Denmark. Coll. and counted by K. LARSEN, 7 June 1953. C.	COOK (1962)
"	2n = 32	between Erlangen und Dechsendorf, Franken, Germany. Coll. C. D. K. COOK & D. PODLECH, 1960. C, CGE, LIVU, M.	COOK (1962)
<i>R. peltatus</i>	2n = 48	Holmsley, Brockenhurst, Hampshire, England. Coll. C. D. K. COOK, 1959. LIVU.	COOK 1st report
<i>R. penicillatus</i> var. <i>penicillatus</i>	2n = 32	River Elz, Prectal, Pfalz, Germany. Coll. C. D. K. COOK, 1960. CGE, M. (This plant is sterile and may be hybrid)	COOK (1962)
<i>R. penicillatus</i> var. <i>penicillatus</i>	2n = 48	River Fane, Dundalk, County Louth, Eire. Coll. D. A. WEBB, 1957. LIVU.	COOK 1st report
<i>R. penicillatus</i> var. <i>calcareus</i>	2n = 32	Sigmaringen, Württemberg, Germany. Coll. C. D. K. Cook, 1960. CGE, M.	COOK (1962)

<i>R. penicillatus</i> var. <i>calcareus</i>	2n = 48	Puddletown, Dorset, England. Coll. C.D.K. COOK, 1958. CGE, LIVU.	COOK (1962)
"	2n = 48	Foulmere, Cambridgeshire, England. Coll. C.D.K. COOK, 1959. CGE.	COOK (1962)
"	2n = 48	River Wye, Haddon, Derbyshire, England. Coll. C.D.K. COOK, 1959. LIVU.	COOK 1st report
"	2n = 48	Oberlaus, Glonn, Oberbayern, Germany. Coll. C.D.K. COOK, 1960. CGE, M.	COOK (1962)
<i>R. penicillatus</i> var. <i>vertumnus</i>	2n = 48	Greywell, Hampshire, England. Coll. C.D.K. COOK, 1958. CGE, LIVU.	COOK (1962)
<i>R. aquatilis</i>	2n = 48	Aflandshage, Denmark. Coll. T. SØRENSEN, Sept. 1954. no voucher found.	CHRISTIANSEN in SØRENSEN (1955)
"	2n = 48	Woodwalton Fen, Huntingdonshire, England. Coll. C.D.K. COOK, 1959. CGE, LIVU.	COOK 1st report
"	2n = 48	Castle Donington, Leicestershire, England. Coll. C.D.K. COOK, 1957. CGE, LIVU, M.	COOK (1962)
"	2n = 48	Stretham, Cambridgeshire, England. Coll. C.D.K. COOK, 1957. CGE, LIVU, M.	COOK (1962)

Species	Count	Origin and Voucher	Reported by
<i>R. aquatilis</i>	2n = 48	Tuddenham, Suffolk, England. Coll. C. D. K. COOK, 1959. CGE.	COOK (1962)
"	2n = 48	Markeaton Brook, Quorndon, Derbyshire, England. Coll. C. D. K. COOK, 1959. LIVU.	COOK 1st report
"	2n = 48	Pöcking, Starnberg, Oberbayern, Germany. Coll. C. D. K. COOK & J. POELT, 1960. CGE, LIVU, M.	COOK (1962)
"	2n = 48	Erling, Herrsching, Oberbayern, Germany. Coll. C. D. K. COOK, 1961. CGE, M.	COOK (1962)
"	2n = 48	Formby Moss, Southport, Lancashire, England. Coll. C. D. K. COOK, 1964. LIVU.	COOK 1st report
"	2n = 48	Japan, Origin and voucher unknown	HARA (1952)
<i>R. trichophyllum</i> subsp. <i>trichophyllum</i>	2n = 16	Origin and Voucher unknown.	LANGLET (1927)
"	2n = 16	Delta, Manitoba, Canada. 26th July 1953, LÖVE & LÖVE, 6174 MAN. [B. subrigidus (Drew) Ritchie].	LÖVE & SOLBRIG (1964), LÖVE & SOLBRIG (1965).
<i>R. trichophyllum</i> subsp. <i>trichophyllum</i>	2n = 32	Tarhit, W. Grand Erg, Algeria. Coll. G. REESE, 1955. Voucher?	REESE (1957)

"	2n = 32	Wicken fen, Cambridgeshire, England. Coll. C.D.K. COOK, 1956. CGE, LIVU, M.	COOK (1962)
"	2n = 32	Woodwalton Fen, Huntingdonshire, England. Coll. C.D.K. COOK, 1959. CGE, LIVU.	COOK (1962)
"	2n = 32	River Würm, Obermenzing, München, Germany. Coll. C.D.K. COOK, 1960. CGE, M.	COOK (1962)
"	2n = 32	Ascholding, Oberbayern, Germany. Coll. C.D.K. COOK, 1960. CGE, M.	COOK (1962)
"	2n = 32	Oberstdorf, Allgäu, Germany. Coll. C.D.K. COOK, 1960. C, CGE, M.	COOK (1962)
"	2n = 32	Fischen, Allgäu, Germany. Coll. C.D.K. COOK, 1960. C, LIVU, M.	COOK 1st report
"	2n = 32	Desford, Manitoba, Canada. 15 July 1953, LÖVE & LÖVE 6090. MAN.	LÖVE & LÖVE (1964), LÖVE & LÖVE (1965).
R. trichophyllus subsp. lutulentus	2n = 32	Origin and Voucher unknown.	MATTICK in TISCHER (1950).
"	2n = 32	Iceland. Coll. and voucher unknown.	LÖVE & LÖVE 1956
"	2n = 32	Claverling Island, N. E. Greenland. Coll. T.S. SØRENSEN. Voucher not found.	JØRGENSEN, SØRENSEN & WESTER- GAAD (1958)
"	2n = 32	BW1, S.W. Greenland. Coll. T. SØRENSEN. Voucher not found.	JØRGENSEN et al. (1958)

Species	Count	Origin and Voucher	Reported by
<i>R. trichophyllus</i> subsp. <i>lutulentus</i>	2n = 32	Egedesminde, N.W. Greenland. Coll. T. SØRENSEN. Voucher not found.	JØRGENSEN et al (1958)
"	2n = 32	Sarqaa Valley, N.W. Greenland. Coll. JAKOBSEN. Voucher not found.	BÖCHER & LARSEN (1950)
"	2n = 32	Funtensee, Berchtesgadener Alpen, Germany. Coll. C.D.K. COOK, 1960. CGE, M.	COOK (1962)
"	2n = 32	Geissalpssee, Allgäu, Germany. Coll. C.D.K. COOK & W. GUTERMANN, 1960. CGE, M.	COOK (1962)
<i>R. rionii</i>	2n = 16	Prater, Wien, Austria. Coll. C.D.K. COOK & A. PATZAK, 1960. CGE, LIVU, M, W.	COOK (1962)
"	2n = 16	Himberg, S.E. Austria. Coll. C.D.K. COOK, 1960. C, CGE, M.	COOK (1962)
"	2n = 16	Maqil, Basra, Iraq. Coll. K.H. RECHINGER fil., No. 15808, 16 March 1957. CGE, W.	COOK (1962)
"	2n = 16	Hywair, Iraq. Coll. K.H. RECHINGER fil., No. 8488a, 17 March 1957. W, LIVU.	COOK 1st report
<i>R. sphaerospermus</i>	2n = 16	between Qurna and Madina, Iraq. Coll. K.H. RECHINGER fil., No. 8477, 17 March 1957. CGE, W.	COOK (1962)

R. circinatus	2n = 16	Trenthorster See, Bad Oldesloe, Schleswig-Holstein, Germany. Coll. H. SCHEERER, 1938, no voucher.	SCHEERER (1939)
"	2n = 16	Mydlniki, Krakow, Poland. Coll. ? voucher ?	TURAŁA in SKALIŃSKA (1959)
"	2n = 16	Maków Podhalański, Poland. Coll. ? voucher ?	TURAŁA in SKALIŃSKA (1959)
"	2n = 16	Cheddar, Somerset, England. Coll. H. K. WHITEHOUSE, 1958. CGE.	COOK (1962)
"	2n = 16	Wicken Fen, Cambridgeshire, England. Coll. C. D. K. COOK, 1959. CGE.	COOK (1962)
"	2n = 16	Woodwalton Fen, Huntingdonshire, England. Coll. C. D. K. COOK, 1959. LIVU.	COOK 1st report
"	2n = 16	Hemington, Leicestershire, England. Coll. C. D. K. COOK, 1959. CGE.	COOK (1962)
"	2n = 16	Oberlaus, Glonn, Oberbayern, Germany. Coll. C. D. K. COOK, 1960. CGE.	COOK (1962)
"	2n = 16	Nymphenburg, München, Germany. Coll. C. D. K. COOK, 1960. CGE, M.	COOK (1962)
R. fluitans	2n = 16	Quorndon, Derbyshire, England. Coll. C. D. K. COOK, 1957. CGE.	COOK (1962)

Species	Count	Origin and Voucher	Reported by
<i>R. fluitans</i>	2n = 16	Donaueschingen, Württemberg, Germany. Coll. C. D. K. COOK, 1960. CGE, M.	COOK (1962)
"	2n = 16	River Mjå, E. Scania, S. Sweden, Coll. E. KJELLQVIST & S. O. STRANDHEDE, 1961, LD, LIVU.	KJELLQVIST & STRANDHEDE (1961)
<i>R. fluitans</i>	2n = 24	Schleissheimer Kanal, Dachau, München, Germany. Coll. C. D. K. COOK, 1960, C, CGE, M.	COOK (1962)
<i>R. fluitans</i>	2n = 32	Temple Bridge, Suffolk, England. Coll. C. D. K. COOK, 1958, CGE, M.	COOK (1962)
"	2n = 32	Wicken Fen, Cambridgeshire, England. Coll. C. D. K. COOK, 1959, CGE.	COOK (1962)
"	2n = 32	Whatstandwell, Derbyshire, England. Coll. C. D. K. COOK, 1959. CGE.	COOK (1962)
<i>R. omiophyllus</i> X <i>tripartitus</i>	2n = 40	Holmsley, Brockenhurst, Hampshire, England. Coll. C. D. K. COOK, 1959. LIVU.	COOK 1st report
<i>R. baudotii</i> X <i>aquatilis</i>	2n = 40	Aflandshage, Denmark. Coll. T. SØRENSEN, Sept. 1954, no voucher found.	CHRISTIANSEN in SØRENSEN (1955)
<i>R. aquatilis</i> X <i>trichophyllus</i>	2n = 40	Woodwalton Fen, Huntingdonshire, England. Coll. C. D. K. COOK, 1959. CGE, LIVU.	COOK 1st report

R. peltatus X fluitans	2n = 40	Peakirk, Northamptonshire, England. Coll. C. D. K. COOK, 1958. CGE.	COOK (1962)
R. fluitans X trichophyllus	2n = 24	River Würm, Obermenzing, München, Germany. Coll. C. D. K. COOK, 1960. C, CGE, M.	COOK (1962)
R. fluitans X trichophyllus or aquatilis	2n = 40	Monsal Dale, Derbyshire, England. Coll. C. D. K. COOK, 1957. CGE, LIVU.	COOK (1962)

R. aquatilis and R. peltatus are frequently confused. The following counts of 2n = 32 could refer to either (I have been unable to see voucher specimens.): LARTER (1932), BÖCHER (1938), EHRENBERG (1945), DELAY (1947) and TURALA in SKALIŃSKA (1958).

The chromosome number alone is of limited value in the systematics of the group as, at least, 6 species exist at two or more levels of polyploidy.

An artificial autotetraploid of *R. hederaceus* has been induced with aqueous colchicine solution. The method employed consisted of maintaining a droplet of 0.04 per cent colchicine solution between the cotyledon leaves of the young seedling and allowing the apex to grow through the droplet. To maintain humidity the seedlings were kept in a sealed tank partly filled with water. The treatment lasted four or five days depending upon the growth of the apex. The 0.04 per cent colchicine solution had a profound effect on all seedlings; the rate of growth was slowed down and any new leaves produced were markedly deformed and succulent. Only one polyploid was obtained from 150 treated seedlings.

When diploid and autotetraploid plants of *R. hederaceus* are cultivated side by side in uniform conditions they are easily distinguishable. The autotetraploid is more shiny, somewhat succulent, slower growing with a more compact habit and shows a tendency to become fasciated. Flowering normally starts about two weeks later than the diploid and continues for about two months after the diploid. There is no evidence that the autotetraploid occurs wild in nature.

The naturally occurring diploid and tetraploid plants of *R. omiophyllum* and *R. fluitans* and diploid, tetraploid and hexaploid plants of *R. peltatus* are extremely similar and I have failed to find any gross morphological characters that indicate the level of ploidy. A similar situation has been well described by SOLBRIG (1964): he was unable to distinguish diploids from tetraploids of *Gutierrezia sarothrae* (Asteraceae) after a detailed study of their ecology, geography and 11 morphological characters from 53 wild populations.

When more or less equal-aged plants of each level of ploidy are cultivated side by side under more or less uniform conditions some differences become apparent. Table 1 shows a comparison of diploid and synthesized autotetraploid *R. hederaceus* and diploid and naturally occurring tetraploid of *R. omiophyllum*.

Table 1

	R. hederaceus		R. omiophyllus	
	2n	4n	2n	4n
Stomatal length (μ)	27.5	35.8	26.7	36.1
s. d.	1.7	2.8	1.5	2.1
Pollen diameter (μ)	27.3	33.3	26.9	30.9
s. d.	1.6	2.5	0.5	1.8
Apparent male fertility (%)	99	85	99	96
Female fertility (%)	80	69	74	75
Stamen number	7,8,9, 10,10.	6,9,9 10,11.	8,8,8 10,10.	8,9,9 10,10.
Carpel number	20,24,24, 26,32.	24,27,28, 28,36.	28,30,31, 41,42.	30,34,34, 37,43.

This table was compiled from measurements made on single plants of each species at both diploid and tetraploid levels. The plants in this experiment were cultivated side by side in a cool greenhouse at the Botanic Gardens at München, Germany and gathered in June 1961. Five flowering shoots from each plant were taken. Stomatal length was measured on 25 stomata from one mature leaf from each shoot and the mean and standard deviation (s. d.) calculated. Three anthers from one flower from each shoot were heated in 45 per cent propionic orcein solution. Pollen diameter was measured on 50 well formed grains from each flower. Apparent male fertility was calculated as the percentage of well-formed pollen grains. Female fertility was calculated as an absolute percentage of well-developed achenes in mature heads. Stamen number and carpel number is given for each flower examined. From Table 1 it can be seen that there are considerable differen-

ces between the diploids and the tetraploids of each species.

If, however, these plants are cultivated in different conditions or sampled at different times, the above characters are modified and no clear separation can be made between diploids and tetraploids. For example, figure 30 shows pollen grain diameters of diploid and autotetraploid *R. hederaceus*. The black portions of the vertical lines represent the total ranges, the white portions the standard deviations and the horizontal lines the means. I, II and III represent ramets of a clone of diploid *R. hederaceus* (H-2) while IV and V represent the autotetraploid derived from seeds from this clone. All plants were cultivated at Liverpool University Botanic Garden and gathered on the same day (16 May 1962). I and IV were cultivated terrestrially, side by side outdoors, II and V were cultivated terrestrially, side by side in a cool greenhouse and III was cultivated in 5 cm of water outdoors. Unfortunately, the autotetraploid did not survive in 5 cm of water in this experiment.

It can be seen that plants II and V show a marked difference, I and IV show less difference while III and IV are nearly the same. In this experiment the mean pollen diameter of the aquatically cultivated diploid was slightly greater than that of the terrestrially cultivated tetraploid. A similar situation is found in *R. omiophyllus*. In both species stomatal length is extremely variable and when plants are placed under water the stomatal length in successive leaves may increase or decrease but the environmental factors that induce these changes are not understood. The levels of ploidy of *R. fluitans* and *R. peltatus* are more difficult to determine on morphological criteria. The mere fact that stomatal length, pollen grain diameter, fertility and number of stamens and carpels are plastic and under environmental control precludes the recognition of the level of ploidy from herbarium material.

The determination of the level of ploidy of plants in their natural environments on morphological grounds has been criticised by SOKOLOVSKAYA (1962) who found that pollen diameter was not a good indicator of polyploidy in *Saxifraga*, and SCHWANITZ (1952) who demonstrated that both stomatal size and pollen diameter can be altered by changes in the environment and that this variation may obscure differences due to polyploidy.

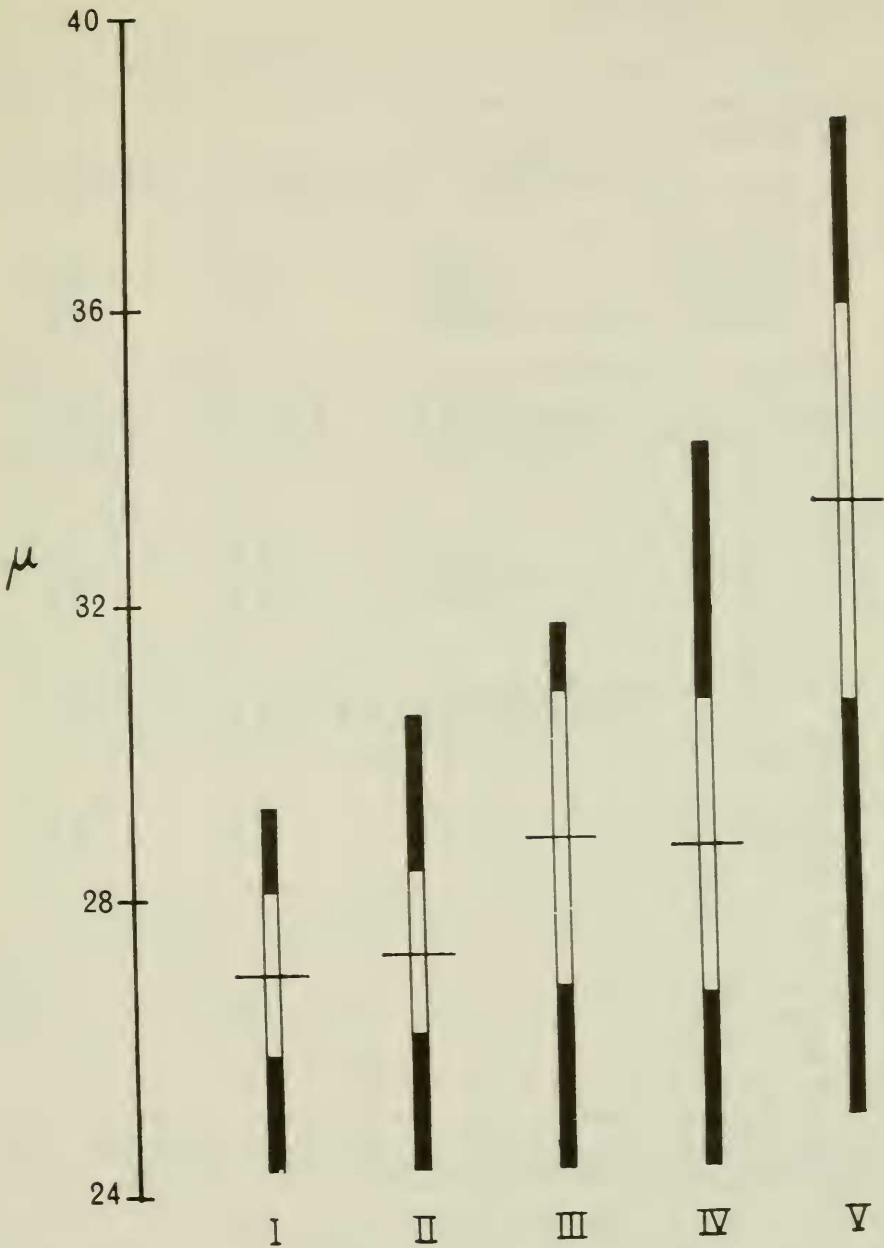


Fig. 30. : Pollen grain diameters of diploid and autotetraploid *R. hederaceus* (see text for explanation).

Chromosome morphology

The karyotype of *Ranunculus* subgenus *Batrachium* is remarkably constant both within and between species. The basic 8 chromosomes can be assigned to three shape categories founded upon the position of the centromere:

1. Meta- or Submetacentric with an arm ratio of 1.0 - 0.75.
2. Acrocentric with an arm ratio of 0.6 - 0.25.
3. Almost Telocentric with an arm ratio of less than 0.2 (excluding satellites).

Absolute chromosome length has little meaning as shrinking agents such as alpha bromo-naphthalene or colchicine had been employed to get better spreading of the chromosomes at metaphase. On a fully shrunken metaphase preparation the longest chromosome is approximately 5 μ and the shortest 2 μ . However, within the karyotype it is possible to assign the chromosomes to three size categories based on the length of the longest arm. For convenience, these will be termed long, medium and short.

Combining the size and shape categories, the basic 8 chromosomes can be represented thus:

Long, meta- or submetacentric	1
Medium, meta- or submetacentric	2
Long, acrocentric	1
Medium, acrocentric	3
Short, almost telocentric	1

This basic set appears to be common to all species of *Ranunculus* subgenus *Batrachium* investigated. Figure 31 illustrates the karyotypes of diploid *R. hederaceus* and diploid and tetraploid *R. omiophyllus*. Other authors such as NEVES (1942) and GREGSON (1965) have recognised more chromosome shape and size categories within the genus *Ranunculus* but I find it impossible to adopt their classifications as there is considerable variation from cell to cell within any individual. The medium-length acrocentric chromosomes, for example, show differences in size and position of the centromere but after examining many preparations the variation appears to be continuous and it is not possible to divide them neatly into comparable pairs. Figure 31 illustrates acrocentric chromosomes arranged in order of descending total length.

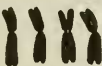
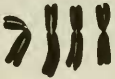
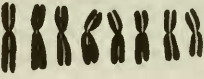
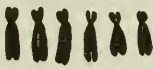
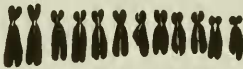
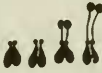
R. HEDERACEUS (H-2)	R. OMIOPHYLLUS (Om-3)	R. OMIOPHYLLUS (Om-2)	
			METACENTRIC (LONG)
			SUBMETACENTRIC (MEDIUM)
			ACROCENTRIC (LONG)
			ACROCENTRIC (MEDIUM)
			ALMOST TELOCENTRIC (SHORT)

Fig. 31. : The Karyotypes of *R. hederaceus* and *R. omiophyllus*.

Satellites are borne on the short arm of the almost telocentric chromosomes and have been seen in all species of subgenus *Batrachium*. Except for the autotetraploid of *R. hederaceus* (H-3) and its hybrids only one pair of these chromosomes bear satellites. The satellites are much larger at prophase than at metaphase and they probably act as nucleolar organizers. In polyploids the extra satellites have probably been lost; loss of satellites in hybrids has been described by NAVASHIN (1934).

The chromosomes of hexaploids are slightly smaller than those of diploids or tetraploids (illustrated in COOK, 1962, fig. 1) but this size difference appears to be controlled by the chromosomal environment as it is not possible to detect the 'smaller' hexaploid chromosomes in hybrids between hexaploids and tetraploids or diploids.

In *Ranunculus* the chromosomes and their morphology have been extensively studied. The following have described, in detail, the karyotypes of different *Ranunculus* species: SOROKIN (1927, 1929), MIYAJA (1927), LARTER (1932), JANE (1932), MATSUURA & SUTÔ (1935), COONEN (1939), NEVES (1942), BAUER (1954), TOMASZEWSKI (1959), KURITA (1957, 1958, 1959, 1960, 1961), BRIGGS (1962), COOK (1962, 1963), GREGSON (1965).

The karyotype of *Ranunculus* subgenus *Batrachium* is in no way extraordinary when compared with the karyotypes of other *Ranunculus* groups. In fact, on the basis of published work the following have karyotypes indistinguishable from *Batrachium*:

R. bulbosus subsp. *adscendens* (Brot.) Neves (*R. adscendens*, KURITA 1958c).

R. bulbosus subsp. *gallecicus* (Freyn ex Willk.) P. W. Ball & Heywood (*R. broteri*, KURITA, 1957b).

R. neopolitanus Ten. (GREGSON, 1965)

R. reptans var. *flagellifolius* (Nakai) Ohwi (KURITA, 1960)

R. hakkodensis Nakai (KURITA, 1957a).

R. ternatus var. *glabra* Boiss. (KURITA, 1957a, 1958c, 1961b).

The Breeding System and Hybrids

The breeding system has been investigated in all the species grown in cultivation (listed in the materials and methods section). All these species have been self-pollinated and found to be self-compatible. They are protogynous and the stigmas are ready to receive pollen 2 - 6 days before the anthers dehisce. *R. trichophyllus* subsp. *lutulentus* appears to be obligately cleistogamous in nature and in cultivation. The other taxa show a tendency to cleistogamy but it is largely under environmental control and is often incomplete. The lower (outer) stamens usually dehisce before the flower bud opens but the released pollen usually reaches only the stigmas of the lower (outer) carpels. As found in many cleistogamous plants the pollen often germinates before the anther dehiscence.

In warm, bright weather the flower normally opens and exposes the stigmas of the unpollinated carpels. Once the flower is open it remains open and does not exhibit nastic movements. The stamens, however, elongate after the flower has opened and eventually the inner stamens shed their pollen over the inner stigmas. The length of time that the unpollinated carpels remain exposed is very variable. In the small-flowered species such as *R. hederaceus* or *R. tripartitus* it may be up to 10 hrs while in the large-flowered species such as *R. peltatus*, *R. penicillatus* or *R. fluitans* it may be up to 48 hrs. In cold or dull weather the flower takes longer to open and pollination is usually complete before the flower opens.

Occasionally, flowers develop under water. When this happens a gas bubble is formed within the closed bud allowing pollination to take place. If a newly opened flower is repeatedly wetted there is a low degree of pollination.

Although there is only a short time for outbreeding under normal conditions, naturally occurring hybrids are by no means rare. The flowers produce visible quantities of nectar and have a sweet-smelling scent somewhat like *Crataegus mongyna* Jacq. but in spite of this no nectar or pollen-taking insects have been seen visiting the flowers. Some chalcids, psychodids, chironomids, *Corixa* sp. and females of *Scopeuma stercorarium* L. have been collected from the flowers and it is possible that they might, by chance, transfer pollen.

In order to cross species of *Ranunculus* subgenus *Batrachium* it is necessary to emasculate the flowers while they are in bud. This is normally done under a microscope as it is very easy to burst an anther or damage the carpels. Polythene tubing sealed with cotton wool is used to prevent foreign pollen reaching the stigmas. Initially, while the flower is erect the polythene tubing is held in position by wire but later after fertilization, when the pedicel starts bending the supporting wire is removed to prevent the pedicel breaking.

Pollen of *R. bulbosus* L., *R. sceleratus* L., *R. ophioglossifolius* Vill., and *Papaver somniferum* L. was placed on the stigmas of *R. hederaceus* (H-2), *R. aquatilis* (A-6) and *R. tripartitus* (Tp-1) to test for pseudogamy in the restricted sense of GUSTAFSSON (1946). The pollen of these species germinated but soon died and no pseudogamy was detected. Embryological investigations were carried out on emasculated flowers but failed to reveal any agamosperous process. It is probable that faulty technique and not apomixis was to blame for the few maternal plants obtained in inter-specific hybrid progenies and from emasculated flowers. Occasionally the periderm develops without fertilization and gives rise to a hollow but externally quite normal looking achene.

Artificially induced hybrids

In the following lists the female parent is cited first. In most cases the hybrid was obtained after the first attempt but in all cases after not more than three attempts. The origins of the parents are listed in the materials and methods section.

1. Fertile hybrids

1. *R. hederaceus* (H-2) X *hederaceus* (H-4)
2. *R. hederaceus* (H-2) X *hederaceus* (H-5)
3. *R. hederaceus* (H-5) X *hederaceus* (H-2)
4. *R. hederaceus* (H-2) X *tripartitus* (Tp-1)
5. *R. omiophyllus* (Om-2) X *tripartitus* (Tp-1)
6. *R. tripartitus* (Tp-1) X *omiophyllus* (Om-2)
7. *R. tripartitus* (Tp-1) X *ololeucos* (Ol-1)

8. *R. tripartitus* (Tp-1) X *peltatus* (Pl-4)
9. *R. tripartitus* (Tp-1) X *peltatus* (Pl-5)
10. *R. baudotii* (B-2) X *hederaceus* (H-3)
11. *R. aquatilis* (A-3) X *aquatilis* (A-6)
12. *R. aquatilis* (A-3) X *penicillatus* var. *vertumnus* (Pnc-1)
13. *R. trichophyllus* (Tt-1) X *trichophyllus* (Tt-2)
14. *R. trichophyllus* (Tt-2) X *trichophyllus* (Tt-1)

2. Sterile hybrids

15. *R. hederaceus* (H-2) X *omiophyllus* (Om-2)
16. *R. hederaceus* (H-2) X *peltatus* (Pl-3)
17. *R. hederaceus* (H-3) X *hederaceus* (H-2)
18. *R. hederaceus* (H-3) X *omiophyllus* (Om-2)
19. *R. hederaceus* (H-3) X *tripartitus* (Tp-1)
20. *R. hederaceus* (H-3) X *trichophyllus* (Tt-1)
21. *R. omiophyllus* (Om-2) X *hederaceus* (H-3)
22. *R. omiophyllus* (Om-2) X *ololeucos* (Ol-1)
23. *R. tripartitus* (Tp-1) X *baudotii* (B-2)
24. *R. tripartitus* (Tp-1) X *peltatus* (Pl-3)
25. *R. baudotii* (B-2) X *omiophyllus* (Om-2)
26. *R. baudotii* (B-2) X *peltatus* (Pl-3)
27. *R. baudotii* (B-2) X *trichophyllus* (Tt-1)

3. Inviabile hybrids

(The number after the hybrid indicates the number of times this particular cross has been attempted).

28. *R. hederaceus* (H-2) X *hederaceus* (H-3) x 2
29. *R. hederaceus* (H-2) X *omiophyllus* (Om-3) x 10
30. *R. hederaceus* (H-2) X *ololeucos* (Ol-1) x 4
31. *R. hederaceus* (H-2) X *baudotii* (B-2) x 2

32. *R. hederaceus* (H-2) X *circinatus* (C-4) x 7
33. *R. hederaceus* (H-2) X *fluitans* (F-2) x 3
34. *R. hederaceus* (H-2) X *fluitans* (F-3) x 2
35. *R. hederaceus* (H-3) X *omiophyllus* (Om-3) x 5
36. *R. hederaceus* (H-3) X *ololeucos* (Ol-1) x 2
37. *R. hederaceus* (H-3) X *circinatus* (C-4) x 2
38. *R. hederaceus* (H-3) X *fluitans* (F-3) x 2
39. *R. omiophyllus* (Om-2) X *hederaceus* (H-2) x 8
40. *R. omiophyllus* (Om-2) X *omiophyllus* (Om-3) x 2
41. *R. omiophyllus* (Om-2) X *peltatus* (Pl-3) x 2
42. *R. omiophyllus* (Om-2) X *aquatilis* (A-6) x 1
43. *R. omiophyllus* (Om-2) X *trichophyllus* (Tt-1) x 2
44. *R. omiophyllus* (Om-2) X *fluitans* (F-3) x 1
45. *R. omiophyllus* (Om-3) X *hederaceus* (H-2) x 10
46. *R. omiophyllus* (Om-3) X *hederaceus* (H-3) x 2
47. *R. omiophyllus* (Om-3) X *omiophyllus* (Om-2) x 3
48. *R. omiophyllus* (Om-3) X *ololeucos* (Ol-1) x 2
49. *R. ololeucos* (Ol-1) X *hederaceus* (H-2) x 3
50. *R. ololeucos* (Ol-1) X *omiophyllus* (Om-3) x 4
51. *R. tripartitus* (Tp-1) X *hederaceus* (H-2) x 12
52. *R. tripartitus* (Tp-1) X *hederaceus* (H-3) x 2
53. *R. tripartitus* (Tp-1) X *aquatilis* (A-6) x 2
54. *R. baudotii* (B-2) X *tripartitus* (Tp-1) x 1
55. *R. peltatus* (Pl-3) X *peltatus* (Pl-4) x 2
56. *R. peltatus* (Pl-3) X *aquatilis* (A-6) x 1
57. *R. peltatus* (Pl-4) X *tripartitus* (Tp-1) x 1
58. *R. peltatus* (Pl-4) X *peltatus* (Pl-3) x 1
59. *R. peltatus* (Pl-4) X *aquatilis* (A-6) x 3

60. *R. trichophyllus* (Tt-1) X *trichophyllus* (Tt-3) x 5

Hybrids 1, 2 and 3. Between geographically separated populations
of *R. hederaceus*

Hybrids 1 (H-2 X H-4), 2 (H-2 X H-5) and 3 (H-5 X H-2) were between plants of *R. hederaceus* collected from England, Germany and Portugal. Batches of 25 F₂ plants have been raised from H-2 X H-4 and H-2 X H-5. The parents and hybrids were all indistinguishable and no differences in fertility have been detected. No evidence has been found to suggest that the parents were not genetically identical and homozygous.

Hybrids 4. *R. hederaceus* (H-2) X *tripartitus* (Tp-1)

This hybrid closely resembled *R. tripartitus* in floral characteristics with its blue sepals and hairy receptacles, but the petals were up to 5 mm long (longer than either parent). The pedicels in fruit did not curve but remained erect. The leaves resembled *R. tripartitus* but had shallower sinuses and more rounded lobes, occasionally, some 5-lobed leaves developed that were indistinguishable from those of *R. omiophyllus*. This hybrid resembled *R. hederaceus* in that it lacked divided leaves and would not tolerate submergence in water. It was a tetraploid with a chromosome number of $2n = 32$. The fertility of this hybrid was low and only about 0.05 per cent of the self-pollinated achenes developed.

Three F₂ plants were raised. They resembled the F₁ in floral characteristics but showed segregation in leaf characteristics; two had leaves that resembled *R. omiophyllus* and had 5 lobes and shallow sinuses, while the third had leaves that resembled *R. tripartitus* and had 3 lobes and deep, straight sinuses. The F₂ hybrids set no achenes. Backcrosses to *R. tripartitus* were attempted but no offspring were obtained.

Hybrid 5. *R. omiophyllus* (Om-2) X *tripartitus* (Tp-1)

Hybrid 6. *R. tripartitus* (Tp-1) X *omiophyllus* (Om-2)

Hybrid 5 and the reciprocal cross hybrid 6 were indistinguishable on morphological characters but differed in fertility. These hybrids resembled *R. tripartitus* except that the petals were

up to 6 mm long, the pedicels remained erect at maturity and the entire leaves were frequently 5-lobed with shallower sinuses and curved lobes. These hybrids were morphologically indistinguishable from some plants found in a few localities in the New Forest, Hampshire, England. These plants are usually called *R. lutarius* by English authors. A full description of this "species" is given in CLAPHAM, TUTIN and WARBURG (1952). This so-called *R. lutarius*, like hybrids 5 and 6, is pentaploid ($2n = 40$) and I have no doubts that it is a hybrid between *R. omiophyllus* and *R. tripartitus*.

The synthesized hybrids exhibited a low fertility. Two plants of Hybrid 6 were reared and one had a fertility of about 9 per cent and the other about 1 per cent, while the only plant of Hybrid 5 that was reared had a fertility of about 3 per cent. (The fertility quoted is the percentage of fertile carpels that develop from self-pollinated flowers). The wild hybrid was sampled from two populations in Hampshire, England; one at Hatchett Pond, Beaulieu and the other at Holmsley, Brockenhurst. In the field there were differences between the two populations; the Hatchett population was smaller-flowered and many plants were heterophyllous while the Holmsley population was larger-flowered and in an entire-leaved state. These plants are highly plastic and when they were cultivated side by side in uniform conditions these morphological differences were no longer apparent, but it was soon noticed that both populations were heterogeneous and each contained individual plants that showed consistent differences in fertility. The lowest fertility was about 7 per cent and the highest about 60 per cent. One plant was chosen, checked to see if it was pentaploid, and then self-pollinated. Ten F₂ offspring were reared and then compared. They were all morphologically alike and pentaploid but showed consistent differences in fertility; the lowest fertility being about 10 per cent and the highest about 55 per cent.

A similar situation was found in the synthesized hybrids. F₂ plants showed no morphological segregation but there were consistent differences in fertility between offspring. However, the progeny derived from the synthetic hybrids was considerably less fertile than those from the wild occurring hybrids. The highest fertility seen in the synthetic F₂ hybrids was about 9 per cent.

It is thought that there may be some agamospermous process at work but its mechanism has not yet been worked out. However, it is unlikely that all achenes are produced apomictically because

when the hybrid is backcrossed, the resulting F₂ shows a bewildering amount of morphological segregation. The following backcrosses have been obtained:

[*R. tripartitus*] X [*Wild (tripartitus X omiophyllus)*].

[*Wild (tripartitus X omiophyllus)*] X [*omiophyllus*].

[*Wild (tripartitus X omiophyllus)*] X [*tripartitus*].

[*Synthesized (tripartitus X omiophyllus)*] X [*tripartitus*].

The following crosses were attempted but no offspring were obtained:

[*R. omiophyllus*] X [*Wild (tripartitus X omiophyllus)*].

[*Synthesized (tripartitus X omiophyllus)*] X [*omiophyllus*].

[*R. tripartitus*] X [*Synthesized (tripartitus X omiophyllus)*].

Figure 32 illustrates the parents, F₁ and some backcrossed segregates. This figure shows that several of the backcrossed hybrids are unlike either of the parents but it does not give a good impression of the amount of segregation as many plants differed in rate of growth and colour. Some F₂ plants were weak while others were robust, some were slow-growing and compact while others were quick-growing and spreading. The colours of the plants were quite remarkable; they ranged from deep purplish-red to light yellowish green and one plant (derived from [*Wild (tripartitus X omiophyllus)*] X [*omiophyllus*]) had yellowish-green leaves with purple petioles and stems. The leaves of *batrachia* are normally green with occasional red patches and the colours seen in these hybrids were unlike any wild species.

Eleven backcrossed hybrids were raised. With so few hybrid plants it is not possible to make any generalisations about the inheritance of any characters except that no character appeared to segregate in a simple manner. Like *R. tripartitus* all plants had blue sepals and hairy receptacles.

The following more complicated crosses have been made and the offspring successfully reared:

[*tripartitus*] X [*tripartitus X Wild (tripartitus X omiophyllus)*].

[*tripartitus X Wild (tripartitus X omiophyllus)*] X [*tripartitus*].

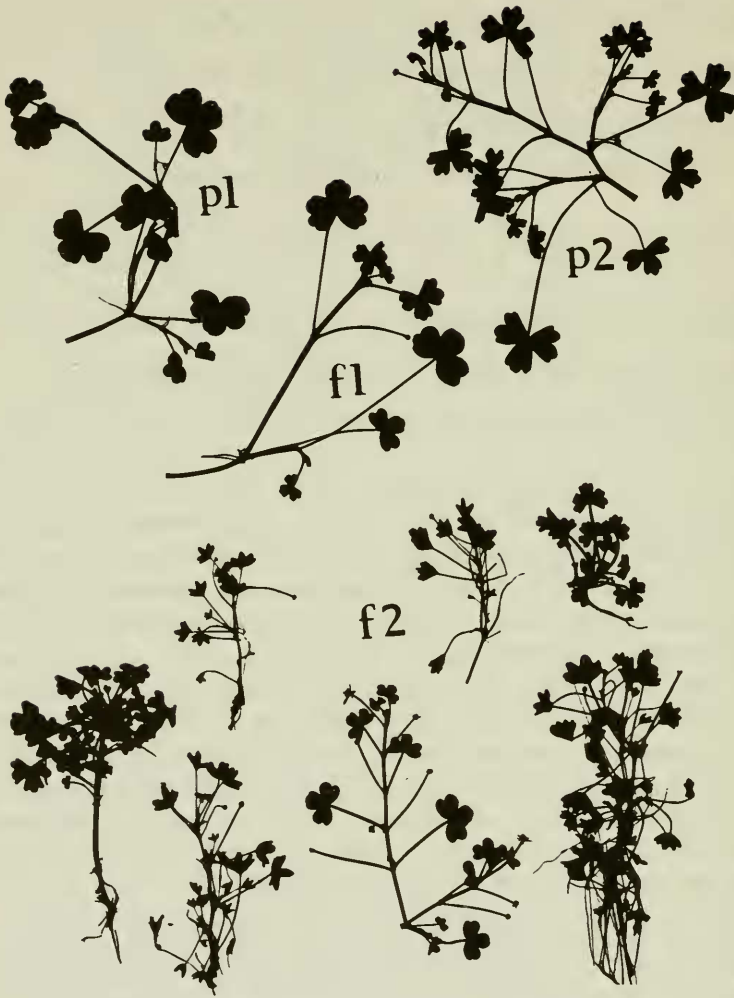


Fig. 32.: *R. omiophyllus* and *R. tripartitus* and their hybrids.
(p1 = *R. omiophyllus*, p2 = *R. tripartitus*, f1 = *R. omiophyllus*
X *tripartitus*, f2 = segregates from the cross p2 X f1).

[tripartitus X Wild (tripartitus X omiophyllus)] X [Wild (tripartitus X omiophyllus)] .

[tripartitus X Wild (tripartitus X omiophyllus)] X [Wild (tripartitus X omiophyllus) X tripartitus] .

The offspring from these crosses showed considerable segregation but it was all within the limits found in backcrossed R. tripartitus X omiophyllus.

The following crosses were each attempted four times but no offspring were obtained.

[Wild (tripartitus X omiophyllus)] X [Synthesized (tripartitus X omiophyllus)] .

[Wild (tripartitus X omiophyllus)] X [Synthesized (omiophyllus X tripartitus)] .

It is interesting that no offspring resulted from these two crosses because, if the wild hybrid develops achenes agamosperously, one would have expected some maternal-like progeny. Each flower contains an average of 25 carpels; 8 crosses were attempted and an excess of pollen was used, so a total of about 200 carpels were pollinated. Normally the maternal parent in these crosses sets about half of its carpels when self-pollinated but, in this case, the pollen must have had very nearly the same genetic constitution as the maternal parent but it would not "induce" the formation of achenes.

Hybrid 7. R. tripartitus (Tp-1) X ololeucos (Ol-1)

In floral characteristics this hybrid was intermediate between those of the parents. The leaves showed instability in form; most leaves were entire and resembled the parental type, but occasionally in short photoperiods divided and intermediate kinds of leaves developed. This leaf-form instability is described in more detail for Hybrids 8, 9 and 10.

This hybrid had an achene fertility of about 0.5 per cent. At the time of writing the F₂ progeny has not reached maturity but it appears that there is segregation in leaf-form similar to that found in hybrid 10.

Hybrid 8. *R. tripartitus* (Tp-1) X *peltatus* (Pl-4)

Hybrid 9. *R. tripartitus* (Tp-1) X *peltatus* (Pl-5)

The plants of *R. peltatus* Pl-4 and Pl-5 were morphologically indistinguishable and were collected about 20 km apart in Hampshire, England. The Hybrids 8 and 9 were indistinguishable. In floral characteristics they were intermediate between those of the parents except that the sepals were blue, nectar-pits lunate and achenes glabrous. These hybrids were somewhat weak and highly unstable in leaf-form. Figure 33 illustrates 5 terrestrially cultivated stems taken from one plant on the same day (23 September 1958). Regardless of the conditions under which the plants were grown divided, intermediate and entire leaves developed intermixed and without sequence. Occasionally stems produced one kind of leaf for ten or more internodes but this was rare and all stems were usually unstable. The variation in leaf-shape was wider than that found in either parent. These hybrids, like their parents, were hexaploid ($2n = 48$) and highly fertile. The fertility varied with the condition of the plant; vigorous shoots had an achene fertility of up to 65 per cent while weak shoots were often sterile. Due to an oversight, no F₂ progeny have been reared.

Hybrid 10. *R. baudotii* (B-2) X *hederaceus* (H-3)

This hybrid was obtained by crossing *R. baudotii* with the synthesized autotetraploid of *R. hederaceus*. The same cross employing diploid *R. hederaceus* has been attempted twice but no fertile achenes were formed.

The flowers of this hybrid were similar to *R. baudotii* and had hairy receptacles and winged achenes but differed in having smaller petals that rarely exceeded 5 mm in length. Most of the leaves were of the intermediate kind but the leaf-form was somewhat variable; the lobes were wide during long photoperiods and narrow during short photoperiods. This hybrid grew most vigorously when cultivated terrestrially and if placed in 25 cm or more of water the stems broke off and floated to the surface. Submergence in water did not modify the kind of leaf that was produced.

This hybrid was tetraploid ($2n = 32$) and fairly fertile; vigorous stems set up to 30 per cent of their achenes. The F₂ exhibited a considerable amount of segregation and, apart from



Fig. 33.: Terrestrially cultivated stems taken from a single plant of *R. tripartitus* x *peltatus*.

intermediate plants that resembled the F1, plants were obtained that were dominantly entire-leaved and terrestrial in habit while others were dominantly divided-leaved and more tolerant of submergence in water. Figure 34 illustrates these three kinds of F2.

The original F1 was obtained in 1959 and the F2 plants were reared in 1960. In 1963, the F1 was again self-pollinated and in 1964, 50 F2 offspring were raised but they showed no segregation. In 1965 another 25 plants were raised from "open" pollinated F1 and they also showed no segregation. It would appear that the F1 may have become agamospermous. At the time of writing the type of agamospermous mechanism remains unknown.

Hybrid 11. *R. aquatilis* (A-3) X *aquatilis* (A-6)

This hybrid was between two morphologically identical but geographically separated plants of *R. aquatilis*. The hybrid was indistinguishable from the parents and fully fertile.

Hybrid 12. *R. aquatilis* (A-3) X *penicillatus* var. *vertumnus* (Pnc-1).

This hybrid was a large robust plant morphologically unlike either of the parents and was intermediate between *R. peltatus* and *R. penicillatus* var. *calcareus*. Like each parent, it was hexaploid ($2n = 48$) and fully fertile. The morphology of this hybrid is useful as evidence that *R. penicillatus* and its varieties are a series of segmental amphidiploids derived from diploid and tetraploid stocks of *R. peltatus*, *R. trichophyllus* and *R. fluitans*. Hexaploid *R. aquatilis* is also an amphidiploid that is probably derived from *R. peltatus*- and *R. trichophyllus*-like stocks.

Hybrid 13. *R. trichophyllus* (Tt-1) X *trichophyllus* (Tt-2)

Hybrid 14. *R. trichophyllus* (Tt-2) X *trichophyllus* (Tt-1)

Hybrid 13 and its reciprocal cross Hybrid 14 were indistinguishable. *R. trichophyllus* (Tt-1) had non-elongating peduncles and very hairy achenes, while Tt-2 had elongating peduncles and achenes of intermediate hairiness (see page 135). The F1 possessed non-elongating peduncles and achenes of intermediate hairiness. The F1 was fully fertile and 10 F2 plants were reared. The F2 plants exhibited a range of achene-types from almost glabrous to densely hairy, indicating that this character is under a form of quantitative inheritance. Nine of the F2 plants had non-



Fig. 34.: Terrestrially cultivated F2 plants of *R. hederaceus* x *baudotii* (A: intermediate-leaved, B: divided-leaved, C: entire-leaved).

elongating peduncles so this character may show a mendelian type of inheritance but as both parents were tetraploid ($2n = 32$) and only ten F₂ plants were reared it is not possible to say more about the inheritance of this character.

Hybrid 15. *R. hederaceus* (H-2) X *omiophyllus* (Om-2)

This hybrid, between diploid *R. hederaceus* and tetraploid *R. omiophyllus*, was a highly sterile triploid ($2n = 24$). Apart from a little more vigour it was indistinguishable from *R. omiophyllus* on gross morphological characters. It had an apparent pollen fertility of 4 per cent but no fertile achenes have been produced. The reciprocal cross has been attempted eight times but no offspring have been obtained. All attempts at inducing a hexaploid from this triploid have, so far, failed.

Hybrid 16. *R. hederaceus* (H-2) X *peltatus* (Pl-3)

Like Hybrids 6, 8, 9 and 10, this hybrid had a somewhat unstable leaf-form. Divided, intermediate and entire leaves were produced when the plant was cultivated terrestrially or submerged during long or short photoperiods. The flowers, however, were usually subtended by the more entire kind of leaf. In size, shape and number of parts the flowers were intermediate between those of the parents, except that the receptacle was hairy and the achenes glabrous. The peduncles remained erect after flowering. This hybrid was diploid ($2n = 16$) and sterile.

Hybrid 17. *R. hederaceus* (H-3) X *hederaceus* (H-2)

This hybrid was the result of a cross between maternal autotetraploid and paternal diploid *R. hederaceus*; the reciprocal cross has been attempted twice without success. STEBBINS (1958) pointed out that in crosses involving diploids and autotetraploids the diploid usually is the poorer maternal parent. This hybrid was triploid ($2n = 24$) and produced no fertile achenes. In summer it closely resembles the diploid parent and in winter the autotetraploid parent. All attempts at inducing a hexaploid from this triploid have, so far, failed.

Hybrid 18. *R. hederaceus* (H-3) X *omiophyllus* (Om-2)

Hybrid 21. *R. omiophyllus* (Om-2) X *hederaceus* (H-3)

Hybrid 18 (autotetraploid *hederaceus* and tetraploid

omiophyllus) and its reciprocal cross Hybrid 21 were highly sterile tetraploids ($2n = 32$) which were morphologically indistinguishable from the triploid hybrid described above (Hybrid 15). Both these tetraploid hybrids had an apparent pollen fertility of about 15 per cent but neither produced mature achenes. This apparently fertile pollen stained well and looked perfectly formed but when used for backcrossing to either parent it would not germinate. Reciprocal backcrosses have been made and parental pollen germinated on the hybrid stigmas but no fertile achenes were formed.

The nature of this hybrid sterility appears to be genic rather than chromosomal. From studies of mitosis there are no visible differences between the karyotypes of *R. hederaceus* and *R. omiophyllus* (fig. 31). During meiosis the tetraploid hybrid shows some univalent formation (fig. 35 A) which is not found in diploid *R. hederaceus* (fig. 35 B). Although the meiotic preparations are far from satisfactory there is no great

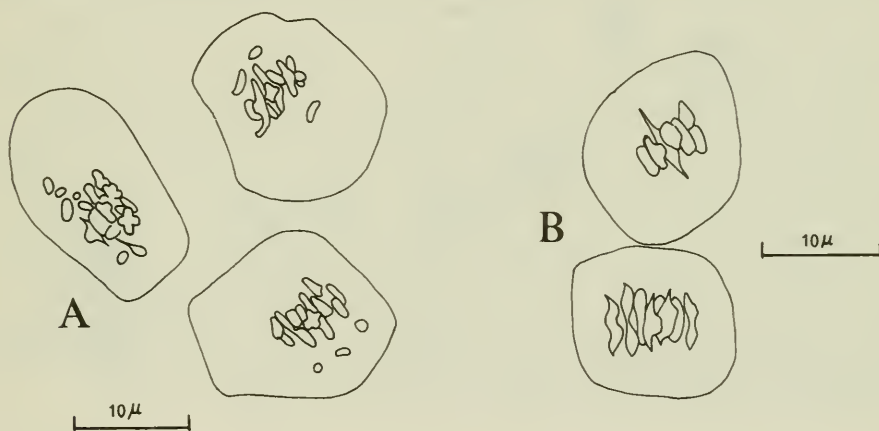


Fig. 35.: P.M.C. meiosis in: A - *R. hederaceus* x *omiophyllus*, B - diploid *R. hederaceus* (H-2).

chromosomal unbalance and hybrids between tetraploid *R. hederaceus* and *R. baudotii* show similar meiotic figures and apparent pollen-fertility but produce fertile achenes which germinate and give rise to F₂ progeny which show segregation. Similar situations have been reported by LAMMERTS (1931) in *Nicotiana* and by GAJEWSKI (1957) in *Geum*. In spite of

repeated attempts no allopolyploids have been induced from these hybrids, so it is not possible to rule out chromosomal sterility. As both diploid *R. hederaceus* and tetraploid *R. omiophyllus* will form fertile hybrids with *R. tripartitus* it looks as if the sterility is genic in nature, especially as the F2 progeny from these hybrids with *R. tripartitus* shows segregation in the degree of fertility.

Hybrid 19. *R. hederaceus* (H-3) X *tripartitus* (Tp-1)

This hybrid between autotetraploid *R. hederaceus* and hexaploid *R. tripartitus* was indistinguishable from Hybrid 4 (diploid *R. hederaceus* X *tripartitus*) except that it was sterile. The reciprocal cross has been attempted twice without success.

Hybrid 20. *R. hederaceus* (H-3) X *trichophyllus* (Tt-1)

This hybrid was a weak, slow-growing plant that resembled neither of the parents nor any other species of *Ranunculus* subgenus *Batrachium*. Figure 36 illustrates both parents and the hybrid. When it is considered that one parent is a terrestrial plant with entire leaves while the other is a submerged aquatic with divided leaves it is not surprising that the hybrid is strange. In many ways the leaves of this hybrid resemble the intermediate leaves of *R. flabellaris* Raf. *R. flabellaris* is in subgenus *Ranunculus* and found in North America. It is amphibious and heterophyllous with divided and entire leaves but the change from one type of leaf to the other is gradual with the formation of many sequentially intermediate leaves. The control and development of these intermediate leaves are described and illustrated by BOSTRACK & MILLINGTON (1962).

Hybrid 22. *R. omiophyllus* (Om-2) X *ololeucos* (Ol-1)

This hybrid was morphologically intermediate between the parents except that the receptacle was hairy and the capillary leaves were entirely lacking.

Hybrid 23. *R. tripartitus* (Tp-1) X *baudotii* (B-2)

This hybrid was heterophyllous with divided, intermediate and entire leaves but the leaf-form was not so unstable as the Hybrids 6, 8, 9 and 10. In winter the leaves are divided and in summer they are entire whether the plant is cultivated terrestrial-

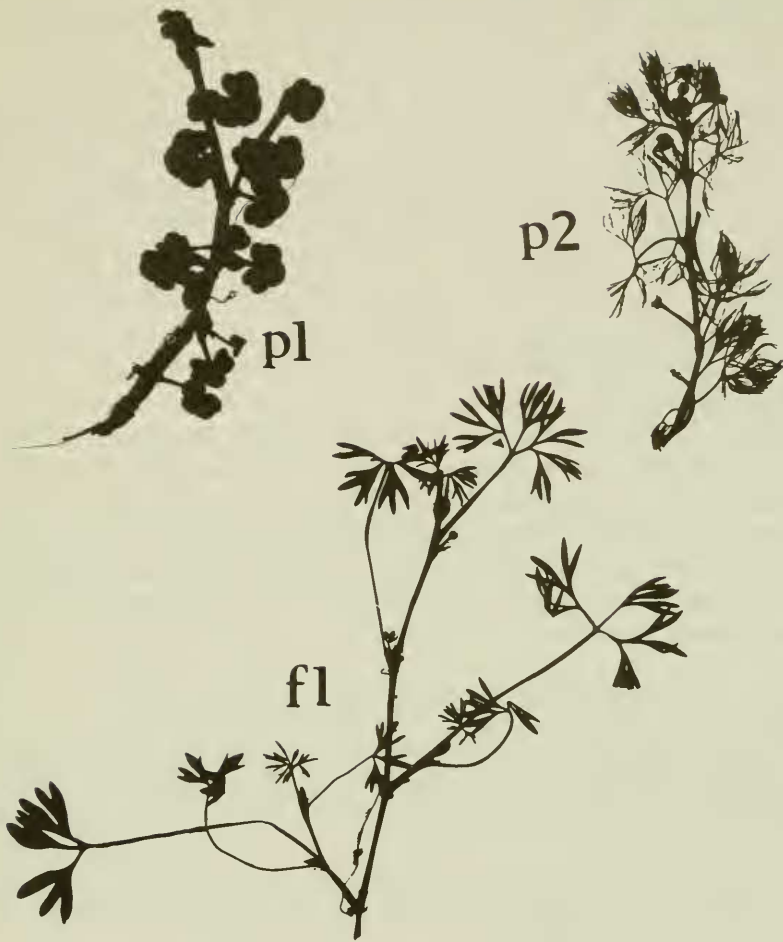


Fig. 36.: p1 = autotetraploid *R. hederaceus* (H-3), p2 = *R. trichophyllus* (Tt-1), f1 = p1 x p2.

ly or submerged. In spring it is possible to see a sequence of leaves from divided to intermediate, to entire. If the plant (including ascending stems) is kept submerged the entire leaves are formed later in the season, and even then they are deeply 3-lobed with very narrow lobes. In autumn there is some instability in leaf-form, and no well defined sequence from entire to divided leaves can be seen. Flowering is not correlated with leaf-form. The flowers are intermediate between the parents. The peduncle does not bend after flowering. The whole plant is a light yellowish-green colour like *R. baudotii* but has the red leaf-patches of *R. tripartitus*. This hybrid is sterile and pentaploid ($2n = 40$).

Hybrid 24. *R. tripartitus* (Tp-1) X *peltatus* (Pl-3)

This hybrid was between *R. tripartitus* ($2n = 48$) and diploid ($2n = 16$) *R. peltatus*. In short photoperiods it resembled Hybrids 8 and 9 (*R. tripartitus* X hexaploid *peltatus*) except that it was sterile but in long photoperiods it lost its leaf-form instability and developed entire leaves only. These entire leaves were 3-or 5-lobed and intermediate in shape between the parents. The flowers were intermediate except that the carpels were completely glabrous.

Hybrid 25. *R. baudotii* (B-2) X *omiophyllus* (Om-2)

In short photoperiods this hybrid developed only divided leaves whether cultivated terrestrially or submerged, but in long photoperiods it formed intermediate and entire leaves and generally resembled Hybrid 10 (*R. baudotii* X autotetraploid *hederaeus*). In size and shape the flowers were intermediate between the parents, but the receptacle was hairy. This hybrid was tetraploid ($2n = 32$) and sterile.

Hybrid 26. *R. baudotii* (B-2) X *peltatus* (Pl-3)

This hybrid looked and behaved like *R. peltatus* except that it was less vigorous, had smaller flowers with glabrous carpels and was sterile.

Hybrid 27. *R. baudotii* (B-2) X *trichophyllus* (Tt-1)

In shape and size the flowers of this hybrid were intermediate between those of parents except that the carpels were hairy. In short photoperiods this hybrid resembled *R. trichophyllus*

but in long photoperiods it developed intermediate leaves of the *R. baudotii* - kind (fig. 3 A). This hybrid was sterile and tetraploid ($2n = 32$).

Naturally occurring hybrids

1. *R. omiophyllus* X *peltatus* [*R. X hiltonii* A. & J. Groves, J. Bot. Lond. 39: 121 (1901)]

This hybrid was first discovered by Mr. T. HILTON at Copthorn Common, Sussex, England in 1896 and, according to WILLIAMS (1926), persisted until, at least, 1926. It was morphologically intermediate between the parents and, when originally discovered, was growing with the parents. In 1956 I visited Copthorn Common and found neither the parents nor the hybrid. This hybrid was curious in that it was highly fertile and showed no leaf-form instability. From herbarium material studied the achenes appeared to contain normal embryos and the pollen contained about 90 per cent of well-formed grains. The well-formed pollen grains were larger than those of either parent. I have been unable to re-synthesize this hybrid but from my experience of crossing closely related species I would have expected this hybrid to be highly sterile and to have an unstable leaf-form. It is possible that *R. X hiltonii* was an amphidiploid that arose from *R. omiophyllus* X *peltatus* and which persisted for, at least, 30 years in one locality but was unable to spread and establish itself elsewhere.

2. *R. omiophyllus* X *tripartitus* [*R. lutarius* auct. Angl.]

This hybrid is described on page 187 .

3. *R. tripartitus* X *ololeucos* [*R. X felixii* Segret, Bull. Soc. Bot. Fr. 72: 782 - 785 (1925)]

This hybrid was discovered by SEGRET at La Ferté-Imbault, Loire-et-Cher, France growing with its parents. Specimens of this hybrid are in Bruxelles Herbarium (BR) "SEGRET, No. 1224, 11 Juin 1924". Morphologically it resembles synthetic hybrid no. 7 but is apparently completely sterile.

4. R. baudotii X aquatilis [R. X lambertii A. Félix, Bull. Soc. Bot. Fr. 59: sess. extr. 63 (1912)].

Detailed accounts of this hybrid are given by ERIKSON (1905) and SØRENSEN (1955). Morphologically it resembles synthetic hybrid no. 27 (R. baudotii X trichophyllum) except that the petals are more obtuse at the apex and the entire leaves are more abundant. It frequently occurs in habitats where both parents grow together. It is completely sterile and, according to SØRENSEN (1955), pentaploid ($2n = 40$).

5. R. baudotii X trichophyllum [R. X segretii A. Félix, Bull. Soc. Bot. Fr. 59: sess. extr. 63 (1912), R. X durandii A. Félix, nom. in schaed. (1913)].

This hybrid resembles synthetic hybrid no. 27 (R. baudotii X trichophyllum). It is of frequent occurrence in localities where the parents grow together. It is a sterile, short-lived annual and has not been seen to persist away from its parents.

6. R. aquatilis X trichophyllum [R. X lutzii A. Félix, Bull. Soc. Bot. Fr. 59: 112 - 120, sess. extr. 61 - 63 (1912), pro parte].

This hybrid is frequently found in localities where R. aquatilis and R. trichophyllum grow together. Morphologically it is intermediate between its parents except that it develops many intermediate leaves of the aquatilis-type (fig. 3b). It is a sterile perennial but has not been found to persist away from its parents. Much of FÉLIX'S material of R. X lutzii in the Herbarium at Bruxelles (BR) is fully fertile and, in my opinion, is referable to either one or other of the parents.

7. R. trichophyllum X circinatus [R. X gluckii A. Félix, nom. in schaed. (1913)].

This hybrid is sterile and morphologically intermediate between the parents. R. trichophyllum and R. circinatus are rarely found sharing a habitat and in consequence the hybrid is of very infrequent occurrence.

8. R. fluitans X peltatus

This hybrid is morphologically intermediate between the parents except that it develops many intermediate leaves of the

peltatus-type (fig. 3 c) and has distinctly hairy receptacles. It is a long-lived perennial that is usually found in flowing water and may live a considerable distance away from its parents. It is normally fully sterile and is believed to be the hybrid that gave rise to the amphidiploid *R. penicillatus* var. *penicillatus*.

9. *R. fluitans* X *trichophyllus* or *aquaticus*

This hybrid is morphologically very variable and probably represents a complex of different hybridizations between diploid or tetraploid *R. fluitans* as one parent and different races of *R. trichophyllus* and *R. aquaticus* as the other. These hybrids are sterile, robust and long-lived perennials that may persist for many years in localities where the parents are not to be found. This may be due to migration of the parents or hybrids.

It is often difficult to predict the parentage of these hybrids. For example, in the River Würm, near München, Germany there is a plant that is a sterile triploid which is morphologically intermediate between *R. fluitans* and *R. trichophyllus*, it is long-lived and has been known in this locality for sixty years. In the same area to-day one finds tetraploid *R. trichophyllus* and triploid *R. fluitans*. The triploid *R. fluitans* has presumably arisen from diploid *R. fluitans* either by fusion of diploid and haploid gametes or by hybridization with tetraploid *R. fluitans*. In this example there is good circumstantial evidence that the parents of this hybrid are *R. fluitans* and *R. trichophyllus*. However, in the River Wye, Monsal Dale, Derbyshire, England there is a sterile pentaploid that morphologically resembles the München triploid. This hybrid is also long-lived and there is a herbarium record of it in the same locality 95 years ago. In this area to-day one finds tetraploid *R. fluitans* and hexaploid *R. aquaticus* so in this example the evidence suggests that *R. fluitans* and *R. aquaticus* are the parents. In spite of this probable difference in parentage the two hybrids are morphologically alike and differ only in chromosome number.

This hybrid complex is particularly interesting as it is believed to have given rise to several different amphidiploid races of *R. penicillatus*. Unfortunately I have not succeeded in synthesizing any of these hybrids. *R. fluitans* does not

flower freely in cultivation so I have had to make experimental pollinations in the field. This has proved unsatisfactory as pollination bags "just disappear" on plants growing in the wild.

Figure 37 is a diagram illustrating the crossing behaviour of all the species of *Ranunculus* subgenus *Batrachium* that have been investigated. All the crosses that have been attempted between diploid species are inviable while crosses between tetraploids and between hexaploids are frequently viable and occasionally fertile. Crosses between hexaploids and diploids or tetraploids are usually viable and frequently fertile. Species that are morphologically alike and often share habitats such as, *R. hederaceus* and *R. omiophyllus*, *R. trichophyllus* and *R. aquatilis*, *R. trichophyllus* and *R. circinatus*,

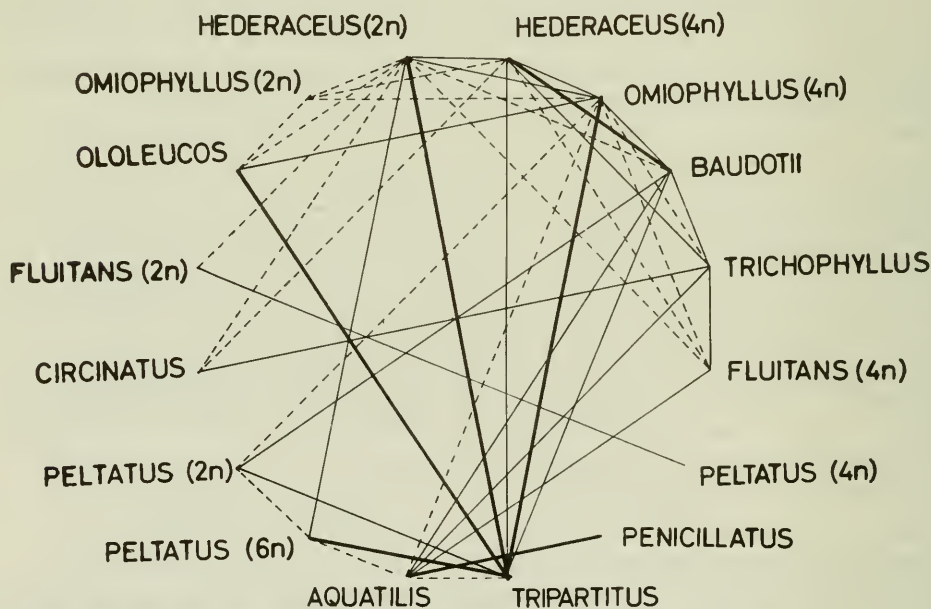


Fig. 37.: Crossing diagram of the species of *Ranunculus* subgenus *Batrachium* (The bold lines represent fertile hybrids, thin lines sterile hybrids and broken lines inviable hybrids).

R. aquatilis and *R. peltatus* and *R. aquatilis* and *R. baudotii*, form inviable or sterile hybrids. Fertile hybrids usually result from crosses between species that would not normally grow close together in nature and that are morphologically somewhat dissimilar. *R. sceleratus*, *R. ophioglossifolius*, *R. bulbosus* and *R. acris* have each been crossed with *R. hederaceus*, *R. omiophyllus* and *R. tripartitus* but all hybrids have been inviable. The lack of any major discontinuities in breeding behaviour within *Ranunculus* subgenus *Batrachium* suggests that this group is monophyletic.

Evolutionary Considerations

There can be no doubt that *Batrachium* is closely allied to the genus *Ranunculus* as the diagnostic features of *Ranunculus* as given by BENSON (1940) are to be found in *Batrachium*. The status of *Batrachium* has varied from a section of *Ranunculus* to genus. It is felt that the level of differentiation shown by this group is sufficient to merit subgeneric rank. The features that are common to all the species of subgenus *Batrachium* are described by COOK (1963). Within the subgenus there are no major morphological discontinuities to suggest that the group is polyphyletic. The uniform karyotype and the ease with which the species hybridize with each other support the hypothesis that subgenus *Batrachium* is monophyletic.

The type of nectary found in *Ranunculus* subgenus *Batrachium* is, according to BENSON (1940), the most reduced type known in the whole genus *Ranunculus* but this reduced nectary is not confined to subgenus *Batrachium*. CHUTE (1930) stated that the batrachian achene represented the most reduced type of any known. She said "so complete is this reduction that the ventrals, as distinct bundles, have completely disappeared; hence the ovule trace appears to come from the dorsals." The vascular anatomy of so few species of *Ranunculus* has been studied that it is uncertain whether the lack of ventral bundles is confined to subgenus *Batrachium*. Regarding the genus *Ranunculus* as a whole, it is fair to state that the nectary and the achene vascular anatomy show reductions. Reduced organs are particularly common in aquatic plants and ARBER (1920) points out that they should be regarded as specialisations for the aquatic environment rather than indicators of

primitiveness. To add weight to arguments supporting the primitiveness of any characteristic some palaeontological evidence is necessary. The earliest fossil record of subgenus *Batrachium* is from the Tiglian interglacial period in Holland (REID, 1907). This interglacial period is usually considered to be the first. The batrachian remains were parts of the lateral walls of the achene and, unfortunately, unidentifiable at the species level.

The present geographical distribution of *Batrachium* suggests a fairly wide pre- or interglacial distribution. On a world-wide basis subgenus *Batrachium* is sympatric with the rest of *Ranunculus*, but *Ranunculus* excluding *Batrachium* is found in Argentina, New Zealand, Malesiana and the central plateau of Africa. Figure 38 A shows an isoporien map (SCHWARZ, 1938) illustrating species density of *Ranunculus* subgenus *Batrachium* and figure 38 B an isosephen map illustrating the distribution of different leaf-types. The distributions shown on these maps are semi-diagrammatic for the sake of simplicity and the boundaries are not as smooth as illustrated. From figures 38 A and 38 B it can be seen that the largest number of species and the greatest diversity of form are to be found in the Atlantic region of Europe. The wide present day distributions of *R. aquatilis*, *R. trichophyllus* and *R. circinatus* suggest that the subgenus may have had a wide pre- or interglacial distribution. Taking into consideration our present knowledge of the geological history of Atlantic Europe, it is better to regard this region as an area of secondary species formation in subgenus *Batrachium*. There is no evidence that suggests that the original evolutionary divergence of the subgenus took place in this region.

Assuming that subgenus *Batrachium* evolved to the aquatic environment from stocks that, to-day, would be recognisable as *Ranunculus*, no process of elaboration of any structure found in *Batrachium* is necessary as all the specialised organs associated with the aquatic environment that are shown in this group are already present in other species of *Ranunculus*. Most of the morphological features common to all the species of subgenus *Batrachium* may be regarded as reductions of existing features found in *Ranunculus* except, perhaps, the stipules. Most terrestrial species of *Ranunculus* have expanded leaf-bases but not distinct and separate stipules. The aquatic species of *Ranunculus* such as, *R. polyphyllus*, *R. flabellaris* and subgenus *Batrachium* show well developed

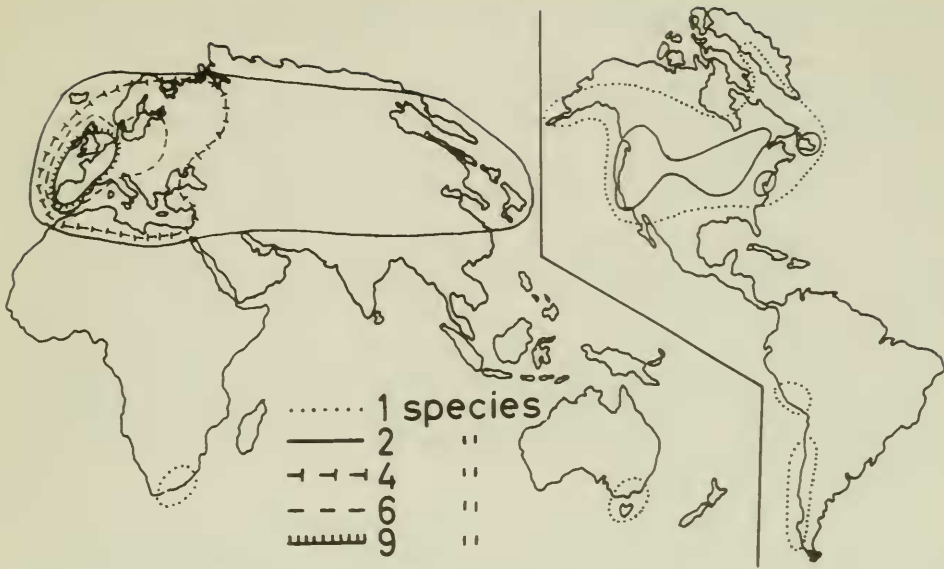


Fig. 38 A.: An isophorien map illustrating species density in *Ranunculus* subgenus *Batrachium*.

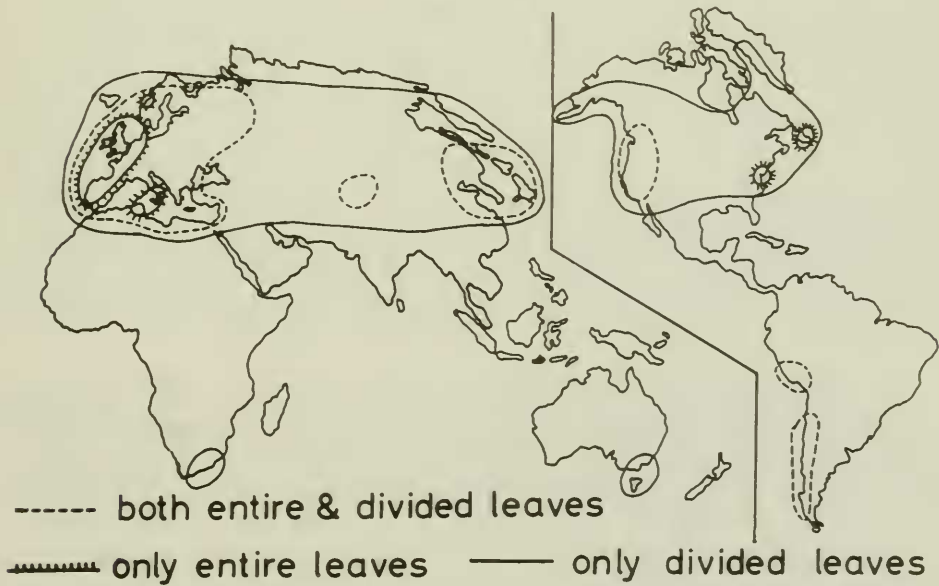


Fig. 38 B.: An isoseperien map illustrating morphological diversity in *Ranunculus* subgenus *Batrachium*.

stipules that, during ontogeny, anticipate the development of the leaf proper. Many aquatic plants have elaborate stipules that are not seen in their terrestrial relatives and one can only assume that stipules have some selective advantage in the aquatic environment. The stipules of aquatic plants are nearly always non-photosynthetic and enclose the stem apex so it is probable that they serve as a protection for the developing leaves and stem.

The divided leaves found in subgenus *Batrachium* are palmate and can be derived from the expanded type of leaf found in *Ranunculus* by reduction of the lamina or accelerated growth of the veins. The tips of the segments of the divided leaves, however, bear hydathodes that, according to MORTLOCK (1952), are non-functional. The presence of these non-functional hydathodes may be further evidence that the divided leaves have evolved from terrestrial leaves.

Most plants that normally occupy both the submerged and terrestrial environments during their generative history usually exhibit a certain degree of heterophylly. The control of this heterophylly varies considerably from species to species. In species such as *Hippuris vulgaris* (DALE & McCULLY, 1961) and *Ranunculus flabellaris* (BOSTRACK & MILLINGTON, 1962) the form of the leaf is more or less directly influenced by various environmental stimuli. In these species the intensity and direction of the environmental stimuli affect the intensity and direction of the phenotypic responses so these species exhibit a great deal of flexibility in leaf-form. Other species such as *Sagittaria sagittifolia* (GOEBEL, 1880, 1895) and *Proserpinaca palustris* (McGALLUM, 1902 & BURNS, 1904) exhibit a heterophylly that is a manifestation of a maturity sequence and is often called heteroblastic development. In heteroblastic plants the leaf-form is hardly influenced by small changes in the environment as long as they do not upset the general metabolism of the plant and thus influence the maturity sequence.

The heterophyllous species of *Batrachium* fall between the direct and heteroblastic morphogeneses as the change from divided to entire leaves is initiated by a photoperiodic stimulus. This stimulus is environmental but its intensity and direction do not affect the intensity and direction of the response. The photoperiodic stimulus merely activates a "switch" or autoregulatory mechanism that changes the leaf morphogenesis from one kind to another. Other environmental stimuli such as temperature, depth

of submergence or water currents have little or no effect on the kind of leaf that develops as long as the general metabolism of the plant is not upset.

Over many generations an autoregulatory morphogenetic mechanism that is tied to a dependable environmental stimulus, such as photoperiod, is probably more reliable in maintaining a high level of adaptation in plants that occupy a constantly changing environment. Plants that respond directly to small changes in the environment are always one step behind the environment. With an autoregulatory morphogenesis some plants should, by chance, anticipate changes in the environment. When this happens these plants should be at an advantage and they are more likely to survive and reproduce. If this is the case, then there should be a selective pressure favouring the autoregulatory-type of morphogenesis in plants that live in changing environments. In regions where there are annual changes in the climate the majority of plants keep in step with or anticipate these changes by autoregulatory mechanisms. For example, most deciduous trees, in their native habitats, drop their leaves before the frosts of winter by adopting autoregulatory morphogenetic mechanisms that are tied to reliable environmental stimuli. The batrachia are exceptional in that they keep in step with or anticipate environmental changes in space with a stimulus that is associated with changes in time.

After discussing the possible advantages of switching directly from divided to entire leaves it is, perhaps, worth speculating on the significance of possessing two types of leaf. The divided leaves, I believe one can accept, are special adaptations that are particularly suited to the submerged environment as similar types of leaves are found in many unrelated taxa of aquatic plants. ARBER (1920) describes and discusses the function of submerged leaves of many aquatics and, more recently GESSNER (1940) has produced some evidence that the divided leaves of *R. baudotii* are particularly well suited to their environment.

The species that have entire leaves that are under autoregulatory control are also the species that are usually found in shallow water (1 m or less). HENSLOW (1908) and others have regarded the entire leaves as structures that enable these species to reap the benefits of the terrestrial environment. In *R. baudotii*, *R. peltatus*, *R. aquatilis* and *R. penicillatus* this is not the case as the entire leaves are confined to the air-water interface and develop only from buds below the water sur-

face. The leaves that develop from buds above the water surface, the truly aerial leaves, are of the divided kind (see page 70). The air-water interface should be considered a distinct environment different from the aerial and submerged ones and many plants such as *Azolla*, *Salvinia*, *Hydrocharis morsus-ranae* and *Lemna* are confined to this environment. It is my belief that the entire leaves of *R. baudotii*, *R. peltatus*, *R. aquatilis* and *R. penicillatus* are special adaptations to this environment and serve as organs that enable these species to compete with other plants that occupy this particular environment.

R. tripartitus, *R. lobbii*, *R. ololeucos* and *R. saniculifolius* are heterophyllous but the entire leaves may develop aerially while *R. hederaceus* and *R. omiophyllus* lack the ability to develop divided leaves and develop entire leaves aerially or submerged. MOSS (1920) and others have regarded *R. hederaceus* and *R. omiophyllus* as the most primitive species on the basis that they lack divided leaves and possess glabrous achenes and receptacles. To-day one tends to regard loss of hairs as an advanced character. Most aquatic plants are glabrous so it is indeed strange that the two terrestrial species of *Batrachium* should be glabrous while nearly all the truly aquatic species are hairy. My own view is that these two species have evolved from aquatic species of *Ranunculus* subgenus *Batrachium* by phylogenetic loss of capillary leaves because the leaves are anatomically very similar to the entire leaves of the heterophyllous species and bear stomata above the palisade tissue on the upper surface of the leaf. The stipules are large and show proleptic growth which is a feature of the aquatic and not terrestrial species of *Ranunculus*.

Aquatic plants that are partially emergent are subjected to an extreme disruption in space as the lower parts may be submerged in water while the upper are in air. BRADSHAW (1965) points out that any disruption in space that approaches the size of the individual plant will form a selection pressure favouring phenotypic plasticity. It is a safe generalisation to say that emergent aquatics do show a considerable amount of phenotypic plasticity in many characteristics; GLÜCK (1923, 1924 & 1936), for example, gives many examples. An aquatic ancestry may well explain how, or perhaps where, *R. hederaceus* and *R. omiophyllus* acquired their considerable degree of plasticity, but once acquired, phenotypic responses will require special selection

pressures to restrict them before selection favouring different genotypes can take place.

Peplis portula and *Montia fontana* frequently occupy the same habitat and have essentially the same life-form and ecology as *R. hederaceus* and *R. omiophyllus* but show very different phenotypic response patterns. These are described by GLÜCK (1923). The genera *Peplis* and *Montia* contain no submerged aquatic species nor have they any living aquatic relatives so it is unlikely that they have evolved from aquatic ancestors. This difference in phenotypic response may provide further evidence that *R. hederaceus* and *R. omiophyllus* have retained their phenotypic plasticity from aquatic ancestors.

COOK (1966) has discussed the relationships between *R. hederaceus* and *R. omiophyllus* and concluded that these two species represent a pair of morphologically distinct homozygous strains that have survived from a polymorphic species-group. Because they often grow together it is impossible to suggest any adaptative advantage for any of the differential morphological characteristics. They have retained their identity because they show hybrid inviability at the diploid level and hybrid sterility at the tetraploid level. At the same time, however, they can be regarded as belonging to a single, potential, common gene-pool as they both form fertile hybrids with *R. tripartitus*.

If the entire-leaved species *R. hederaceus* and *R. omiophyllus* have evolved from heterophyllous species by the phylogenetic loss of divided leaves. The next stage in discussion, is to consider the evolution of heterophylly. There can be no doubt that many aquatic heterophyllous species have evolved from very different terrestrial ancestors. *Rorippa amphibia* (Brassicaceae), *Oenanthe fluviatilis* (Apiaceae), *Limnophila aquatica* (Scrophulariaceae), *Megalodonta beckii* (Heliantheae) and *Cotula myriophylloides* (Asteraceae) are good examples of dicotyledonous aquatics that superficially resemble each other in possessing both divided and entire leaves but which show no close patristic affinities. In these examples, the flowers are invariably borne on shoots bearing 'entire' leaves while the divided leaves are found in the juvenile or overwintering phases of growth. The divided leaves, in these examples resemble the entire leaves in their venation and may be regarded as being derived from them by suppressed growth of

the lamina. During the ontogeny of the plant the change from divided to entire leaves is gradual and many sequentially intermediate types of leaf are formed, each intermediate leaf differing only in the amount of lamina that develops between the veins.

Heterophylly is not confined to aquatic plants: it also occurs in terrestrial plants but in these there is a fundamental difference as the divided leaves are more often associated with flowering while the entire leaves are associated with the vegetative phase. Good examples of this kind of heterophylly are to be seen in *Ranunculus arvensis* (Ranunculaceae), *Oenanthe pimpinelloides* (Apiaceae), *Sidalcea malvaeflora* (Malvaceae) and *Scabiosa columbaria* (Dipsacaceae).

ARBER (1919, 1920) has argued that an aquatic environment alone is not responsible for heterophylly but that the occurrence of heterophylly is a prerequisite for the ability of a terrestrial plant to inhabit an aquatic environment. A great many of the terrestrial species of *Ranunculus* show heterophylly with expanded leaves or leaflets at the base and linear leaves or leaflets on the flowering stems so the necessary ancestral stocks for the evolution of *Batrachium* were probably available.

The heterophyllous batrachia show what must be an evolutionary advance over other recently evolved aquatic plants in that they ontogenetically switch directly from divided to entire leaves by an autoregulatory mechanism. This is regarded as an advance because the species must first have acquired heterophylly under a dependant or a heteroblastic type of morphogenetic control in which sequentially intermediate leaves were developed. The evolution of autoregulatory morphogenetic controls is discussed, in detail, by SCHMALHAUSEN (1949).

Some hybrids, such as *R. hederaceus* X *trichophyllus* and *R. omiophyllus* X *baudotii*, develop leaves that are intermediate in shape between the entire and divided kinds. Such leaves morphologically resemble the intermediate leaves of the heteroblastic, heterophyllous plants but they are not developed in any ontogenetic sequence. Nevertheless, the formation of intermediate leaves is evidence that some species of *Batrachium* possess the necessary morphogenetic pathways for intermediate leaves to develop so it is possible that ancestral stocks may well have shown an ontogenetic sequence of leaves that bridged the gap between the divided and the entire kind.

The heterophyllous species of *Batrachium* show a graduation, in habit, from dominantly terrestrial to dominantly aquatic.

TERRESTRIAL

Predominantly
entire-leaved

| *R. tripartitus* |

| *R. lobbii* |

| *R. ololeucos* |

| *R. baudotii* |

| *R. saniculifolius* |

| *R. peltatus* |

| *R. aquatilis* |

| *R. penicillatus* |

AQUATIC

predominantly
divided-leaved

Fig. 39.

Figure 39 shows a sequence of species that starts with the most terrestrial (predominantly entire-leaved) and follows through to the most aquatic (predominantly divided-leaved). This sequence should not, however, be regarded as an evolutionary trend as some heterophyllous species show closer affinities to non-heterophyllous species. For example, *R. sphaerospermus* differs from *R. peltatus* only in its lack of entire leaves, smaller achenes and the receptacle that elongates in fruit. It is believed that the smaller achenes and elongating receptacles have arisen in three separate lines. These two characteristics are correlated in development and may be no more than different manifestations of a single morphogenetic process and that in each line its occurrence represents homologous variation in the sense of VAVILOV (1922). If this is the case then *R. sphaerospermus*

probably evolved from *R. peltatus*, *R. flavidus* from *R. aquatilis* and *R. rionii* from *R. trichophyllus*.

The evolution of non-heterophyllous, divided-leaved species from heterophyllous ones is a logical development in the evolution of obligate aquatic plants from terrestrial or amphibious ancestors and is seen in many genera such as *Cabomba*, *Myriophyllum*, *Proserpinaca*, *Limnophila* and *Hydrophila*. Which all contain, like *Ranunculus* subgenus *Batrachium*, heterophyllous and non-heterophyllous species.

Figure 40 illustrates the evolution of the different kinds of leaf-arrangement found in *Ranunculus* subgenus *Batrachium*. A is a diagrammatic representation of a terrestrial, heteroblastic species which has entire basal leaves and sequentially inter-

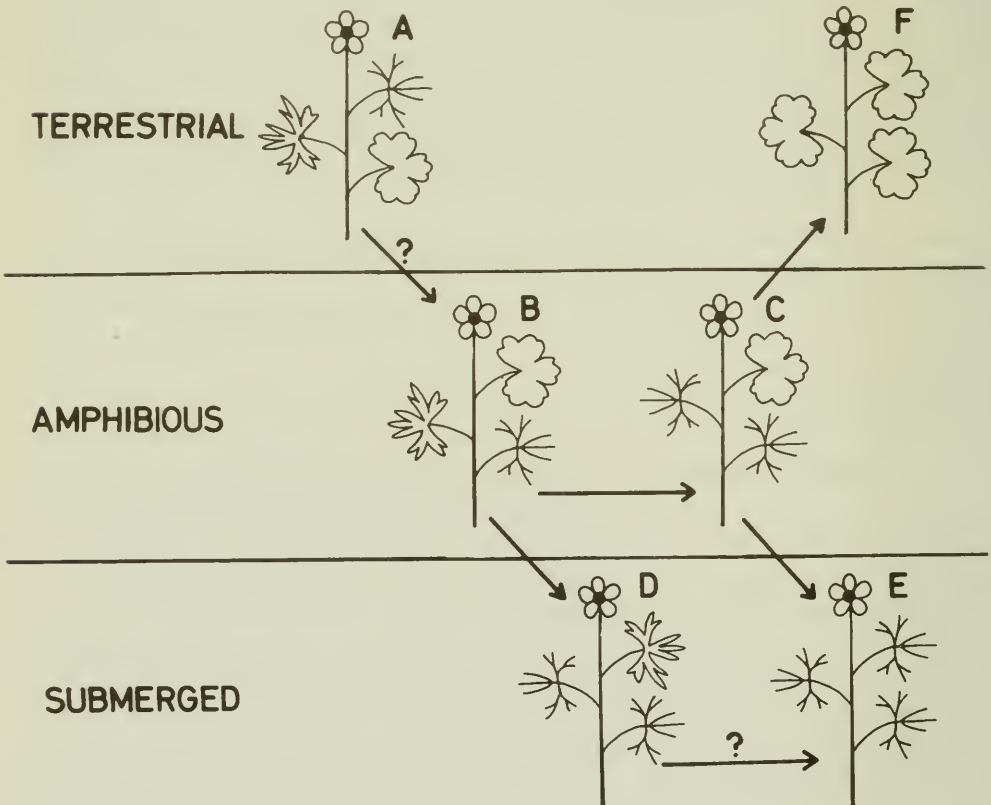


Fig. 40.: The evolution of the different kinds of leaf-arrangement found in *Ranunculus* subgenus *Batrachium* (explanation in the text).

mediate and divided cauline leaves. This kind of heterophylly is not seen in any species of *Batrachium* but is found in many terrestrial species of *Ranunculus* and it may have led to the type of heterophylly seen in B. B represents what is believed to be the ancestral, amphibious heteroblastic species which has divided leaves at the base and intermediate and entire leaves on the flowering stem. This kind of heterophylly is not seen in any species of *Batrachium* at the present time. C represents a heterophyllous species in which the development of sequentially intermediate leaves is suppressed. All heterophyllous species of *Batrachium* show this kind of heterophylly. D represents an aquatic species that has evolved from B. It is believed that *R. fluitans* may have evolved in this way as it occasionally develops intermediate leaves on flowering stems. E represents an aquatic species that has evolved from C by phylogenetic loss of entire leaves or from D by phylogenetic loss of intermediate leaves. *R. trichophyllus*, *R. rionii*, *R. sphaerospermus* and *R. flavidus* are believed to have evolved in the former way and *R. circinatus* and *R. longirostris* in the latter. F represents a secondarily terrestrial species that has evolved by phylogenetic loss of divided leaves. *R. hederaceus* and *R. omiophyllus* are believed to have evolved this way.

Hybridization in the present day species of *Batrachium* sheds little light on the genetic similarities of the existing species so that phylogenetic relationships must be largely speculative. However, the nature of hybrids formed does occasionally give an insight into the mechanisms of species formation. In the cases where the hybrids are fertile it is seen that the variation obtained in the F₂ is far greater than that seen in either of the parents. For example, the F₂ progeny from *R. hederaceus* X *R. baudotii* fell into three categories: heterophyllous, entire-leaved and divided-leaved. As one parent was entire-leaved and the other heterophyllous it can be seen that the divided-leaved progeny were unlike either parent and thus pre-adapted for an environment unsuitable for either parent. Therefore new levels of adaptation may arise extremely quickly.

Hybridization, in this group, releases an enormous amount of transgressive variation. Natural selection will favour those biotypes that are best suited to a particular environment. If the particular environment is, at that moment, unexploited the process of colonization of new biotypes may be very rapid. As essential-

ly similar environments become exploited by different biotypes there will be strong competition between the biotypes that are most similar in their demands on that environment. Any barriers that may arise which limit free exchange of genetic material between these biotypes will accelerate the formation of new species. Therefore the species that are genetically and morphologically most similar are likely to be separated by a genetic barrier so that the apparent paradox, that the closest related species are unable to exchange genetic material while the more distant relatives may, becomes a reality.

Spatially isolated plants are more likely to be morphologically dissimilar especially if there is any ecological separation. But because of transgressive variation a morphological dissimilarity may not reflect a great genetic difference in *Batrachium*. If plants are spatially isolated there is no selection pressure favouring the erection of genetic barriers to limit gene-flow so, when crossed, these plants will, once more, release a mass of genetic variation. This recurrent hybridization is only likely to occur while there are unexploited habitats available so that plants normally separated may come together to hybridize.

This recurrent hybridization may explain the origin of *R. hederaceus* and *R. omiophyllum* as these two species are morphologically very similar and often share the same habitat but are prevented from crossing by a genetic sterility barrier. This sterility barrier, however, affects only these two mutual species as they are both able to exchange genetic material with the normally spatially isolated species *R. tripartitum*.

The karyotype is remarkably uniform from species to species and sheds no light on the relationships of the species within subgenus *Batrachium*. Chromosome number is also of limited use as several species exist at more than one level of ploidy. However, when chromosome number is considered together with breeding behaviour and general morphology there is evidence that *R. penicillatus sensu lato* represents a collection of segmental amphidiploids that have arisen from hybrids between *R. fluitans* and *R. peltatus*, *R. aquatilis* and *R. trichophyllum*. On morphological grounds it is frequently difficult to predict the parentage of these amphidiploids. It is possible that this difficulty arises because the original hybridization took place before the parents had reached their present identities.

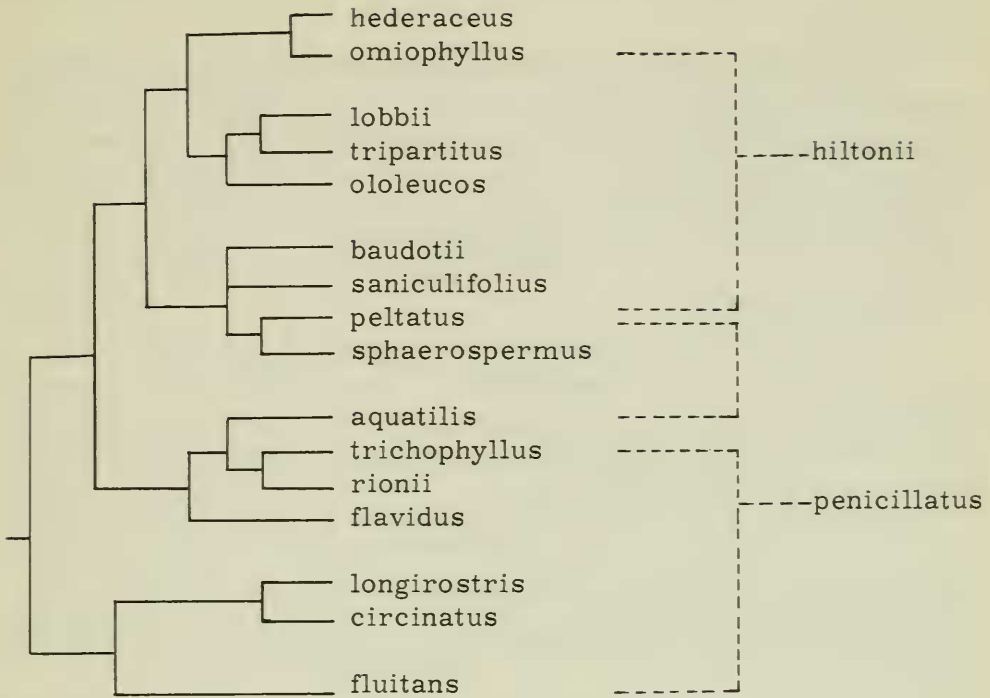


Fig. 41

Figure 41 is presented as a summary. It illustrates what I believe to be the genetic similarities between the present day species of *Ranunculus* subgenus *Batrachium*. This diagram should not be construed as representing a phylogenetic tree. The horizontal axis represents different levels of genetic similarity so that the species that are most closely linked by vertical lines are those that are patristically most closely related. The branching lines trace the phylogenetic history in terms of levels of genetic change but they do not illustrate an absolute time scale. For example, the present day geographic distribution of *R. trichophyllus* and *R. aquatilis* suggests they are old species but just because they are old does not mean that they are necessarily genetically more dissimilar than recent species. The species on the vertical axis are arranged in what appear, on gross morphological grounds, to be the closest phenetic groupings. Amphidiploids are connected to their parent species by dotted lines.

Summary

The evidence from studies on general morphology, cytology and genetic resemblance indicates that *Ranunculus* subgenus *Batrachium* is monophyletic. The original differentiation of the group has not depended upon the origin of new genetic material but merely on the selection of features already present in the genus *Ranunculus*. New biotypes produced by fortuitous recombination of genetic material are assumed to have been subjected to natural selection.

The present distribution of the subgenus suggests that the group evolved in pre- or inter-glacial times. The earliest remains are considered to be from the first inter-glacial period. There is no evidence as to the geographical position of the centre of origin of the group but the Atlantic region of Europe is, today, the centre of both morphological diversity and species density. This region is thought to be a site of secondary speciation resulting from natural selection working on a variety of biotypes formed from the hybridization of previously isolated strains. This secondary speciation is most likely to have taken place in inter- or early post-glacial times.

The phylogeny of the present species is extremely difficult to elucidate as experimental work has indicated that selection following hybridization leads very quickly to new levels of adaptation and that the species that are represented to-day may have undergone several cycles of hybridization and selection. There is also the difficulty that the species that resemble each other the most are also the species that are most likely to compete with each other. Direct competition between closely related species favours the establishment of barriers that prevent the free exchange of genetic material so that it becomes increasingly difficult to establish the degree of genetic affinity between species.

The evolution of the habit within subgenus *Batrachium* is less open to speculation and it is argued that the entire-leaved species have evolved from autoregulatory-controlled ones, and that autoregulatory-controlled heterophylly has evolved from dependent or heteroblastic heterophylly. The divided-leaved species have evolved from both heteroblastic and autoregulatory heterophyllous species.

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Index of Plant Names

The names adopted in this revision are underlined. The numbers on the right hand column refer to the numbers assigned to each species in the text. The legitimate names under *Batrachium* at generic rank are marked with a cross.

Batrachium

admixtum Nyl.	= 12a
+ aquatile (L.) Dumort.	= 10
var. grandiflorum Groves	= 8
var. micranthum (Wallr.) Kickx	= 3
var. peltatum (Schränk) Dumort.	= 8
var. trichophyllum (Chaix) Spach	= 12
aspergillifolium Dumort.	= 12
bachii Wirtgen	= 12 x 16
bakeri Greene	= 10 or 12
+ baudotii (Godron) F. Schultz	= 6
bipontinum F. Schultz	= 12
caespitosum (Thuill.) S. F. Gray	nom. incert.
capillaceum (Thuill.) Bercht. & Presl.	nom. incert.
carinatum Schur	
cesatianum Caldesio	= 8
+ circinatum (Sibth.) Spach	= 14
coenosum (Guss.) Nyman	= 2
confervoides Fr.	= 12a
confusum (Godron) Garcke	= 6
dichotomum Schmalh.	= 8
drouetii (F. Schultz) Van den Bosch.	= 12
eradicatum (Laest.) Fr.	= 12a
+ flavidum Hand.-Mazz.	= 11
floribundum (Bab.) Dumort.	= 8
+ fluitans (Lam.) Wimmer	= 16
fluviatile (Wigg.) S. F. Gray	= 16
foeniculaceum (Gilib.) Krecz.	= 14
gilibertii Krecz.	= 10
godronii Gren.	= 10
+ hederaceum (L.) S. F. Gray	= 1
kauffmannii (Clerc) Krecz	= 12
langei F. Schultz	= 8
lenormandii F. Schultz	= 2
lobbianum Gelert	nom. incert.
+ lobbii (Hiern) Howell	= 4

+ longirostre (Godron) F. Schultz	= 15
lusitanicum (Frey) Nyman	= 5
lutarium Revel	= 3
marinum Fr.	= 6
minimum Schur	= 12
mongolicum (Kryl.) Krecz.	= 10
obtusiflorum (DC.) S. F. Gray	= 6
+ ololeucos (Lloyd) Van den Bosch	= 5
+ omiophyllum (Ten.) C. D. K. Cook	= 2
pachycaulon Neviski	= 17
paucistamineum (Tausch) F. Schultz	= 12
var. divaricatum (Schrank) Gelert	= 12
var. diversifolium (Gilib.) Gelert	= 8 or 10
var. drouetii (F. Schultz) Gelert	= 12
var. eradicatum (Laest.) Gelert	= 12a
pedunculare Green ex C. F. Baker	= 12
peltatum (Moench) Bertch. & Presl.	= 10
+ penicillatum Dumort.	= 17
petiveri (Koch) F. Schultz	= 6
peucedanifolium (Ehrh.) Dumort.	= 16
porteri (Britton) Britton	= 12
pumilum (Poir.) Nyman	nom. incert.
radians (Revel) Desmoulins	= 10
+ rhipiphyllum (Bast.) Dumort.	= 8
subsp. sphaerospermum (Boiss. & Blanche) C. D. K. Cook	= 9
rigidum (Persoon) Dumort.	nom. incert.
+ rionii (Lagger) Nyman	= 13
+ saniculifolium (Viv.) Dumort.	= 7
tenellum (Viv.) Dumort.	= 7
+ trichophyllum (Chaix) Van den Bosch	= 12
+ subsp. lutulentum (Perrier & Sogéon) Janchen	= 12a
subsp. rionii (Lagger) C. D. K. Cook	= 13
trinacrium (Huet) Nyman	= 8
tripartitum (DC.) S. F. Gray	= 3
triphyllus (Wallr.) Dumort.	= 8 or 10
truncatum (Koch.) Dumort.	= 8
villosum F. Schultz	= 12

Ranunculus

abrotanifolius (Ehrh.) Steudal	= 12
affinis F. Schultz	= 12

<i>allophyllus</i> Bast.	= 10
<i>aquaticus</i> Lam.	nom. incert.
<u><i>aquatilis</i> L.</u>	= 10
subsp. <i>abrotanifolius</i> Ehrh.	= 12
subsp. <i>marizii</i> Cout.	= 17
subsp. <i>mongolicum</i> Kryl.	= 10
subsp. <i>peucedanifolius</i> Ehrh.	= 16
subsp. <i>trichophyllus</i> (Chaix) Moore & More	= 12
var. <i>bakeri</i> (Greene) Jepson	= 12
var. <i>baudotii</i> (Godron) Crépin	= 7
var. <i>brachypus</i> Hooker & Arn.	= 12
var. <i>caespitosus</i> (Thuill.) DC.	nom. incert.
var. <i>calvescens</i> (W. Drew) L. Benson	= 12
var. <i>capillaceus</i> (Thuill.) DC.	nom. incert.
var. <i>circinatus</i> (Sibth.) With.	= 14
var. <i>confervoides</i> (Fr.) Lawson	= 12a
var. <i>diffusus</i> With.	= 12
var. <i>drouetii</i> (F. Schultz) Lawson	= 12
var. <i>elegans</i> A. Chabert	= 8
var. <i>elongatus</i> (Hiern) A. Chabert	= 8
var. <i>eradicatus</i> Laest.	= 12a
var. <i>fluviatilis</i> (Wigg.) With.	= 16
var. <i>harrisii</i> L. Benson	= 12
var. <i>heterophyllus</i> (Weber) DC.	= 10
var. <i>heterophyllus</i> Moris	= 8
var. <i>homophyllus</i> Moris	= 2
var. <i>lejospermus</i> Wallr.	= 3
var. <i>lobbii</i> (Hiern) S. Watson	= 4
var. <i>longirostris</i> (Godron) Lawson	= 15
var. <i>macranthus</i> (Tod.) Lojac.	= 7
var. <i>micranthus</i> Wallr.	= 3
var. <i>orbiculatus</i> Schum.	= 14
var. <i>pantothrix</i> (Brot.) Koch	= 12
var. <i>pedunculare</i> (Greene) Jepson	= 12
var. <i>peltatus</i> (Schränk) Koch	= 8
var. <i>phellandrifolius</i> Schum.	= 12
var. <i>porteri</i> (Britton) L. Benson	= 12
var. <i>pseudofluitans</i> Syme	= 17
var. <i>quinquelobus</i> Koch	= 8
var. <i>sajanensis</i> E. Regel	= 12a

var. sphaerospermus (Boiss.)	
& Blanche) Boiss.	= 9
var. stagnatilis (Wallr.) DC.	= 14
var. stagnatilis sensu Hooker	= 15
var. submersus Gren. & Godron	= 8 or 10
var. subpeltatus Hooker	= 8
var. succulentus Koch	= 8, 10 or 12
var. symei Hooker & Arn.	= 6
var. truncatus Koch	= 8
$\propto$ longifolius Rossm.	= 17
β millefolius Miljeblad	= 14
asarifolius Diard	= 1
aschersonii Freyn	= 12
atlanticus Pomel	= 7
baudotii Godron	= 6
subsp. leontinensis (Freyn) Nyman	= 8
bauhinii Tausch	= 8, 10 or 12
bungei Steudel	sp. non satis
caespitosus Thuill.	nom. incert.
calcareus R. W. Butcher	= 17 b
cambricus A. Bennett ex Druce	= 17
capillaceus Thuill.	nom. incert.
capillus-naidis Arv.-Touv.	= 12 a
carinatus (Schur) Freyn	= 10
circinatus Sibth.	= 14
circinatus Auct Amer.	= 15
circinnatoides Arv.-Touv.	= 10
codyanus Boivin	= 12 a
coenosus Guss.	= 2
confervoides	= 12 a
confusus Godron	= 6
curvirostris Freyn	= 12
divaricatus Schrank	nom. incert.
var. eradicatus (Laest.)	
F. N. Williams	= 12 a
diversifolius Gilib.	= 8 or 10
proles floribundus (Bab.)	
Rouy & Fouc.	= 8
proles peltatus (Schrank)	
Rouy & Fouc.	= 8
proles truncatus (Koch)	
Rouy & Fouc.	= 8

var. rhipiphyllus (Bast.) Félix	= 8
drouetii F. Schultz	= 12
dubius Freyn	= 8
x duranii Félix	= 6 x 12
eleophilus Arv.-Touv.	= 8 or 10
elongatus F. Schultz	= 8
flaccidus Persoon	= 12
var. confervoides (Fr.) Hegi	= 12 a
var. parviflorum C. A. Meyer	= 13
var. rionii (Lagger) Hegi	= 13
<u>flavidus</u> (Hand.-Mazz.) C. D. K. Cook	= 11
x felixii Segret	= 3 x 5
floribundus Bab.	= 8
<u>fluitans</u> Lam.	= 16
proles flabellifolius Rouy & Fouc.	= 17
var. bachii (Wirtgen) Wirtgen	= 12 x 16
var. heterophyllus Cosson & Germ.	= 17
fluviatilis Wigg.	= 16
fluviatilis Pursh	= 12
foeniculaceus Gilib.	nom. incert.
friesii Beurl.	= 6
fucoides Freyn	= 7
gelertii E. H. L. Krause	= 6
gluckii Félix	= 12 x 14
godronii Gren.	= 10
grayanus Freyn	= 10
hederaceus L.	= 1
subsp. coenosus (Guss.) Nyman	= 2
proles homoeophyllus (Ten.)	
Rouy & Fouc.	= 2
var. coenosus (Guss.) Cosson	= 2
var. grandiflorus Bab.	= 2
var. homoeophyllus (Ten.)	
Fiori & Paoletti	= 2
var. lobbii (Hiern) Brewer &	
Watson	= 4
hederaefolius Salisb.	= 1
heterophyllus Weber	= 10
subsp. baudotii (Godron) Moore & More	= 6
subsp. peltatus (Schränk) Moore & More	= 8
subsp. pseudofluitans (Syme) Moore &	
More	= 17
x hiltonii Groves	= 2 x 3

hirtissimum Krause	= 12
hydrocharis Spenner	
var. caespitosus (Thuill.) Spenner	nom. incert.
var. capillaceus (Thuill.) Spenner	nom. incert.
var. hederaceus (L.) Spenner	= 1
var. peltatus (Schränk) Spenner	= 8
var. stagnatilis (Wallr.) Spenner	= 14
var. tripartitus (DC.) Spenner	= 3
var. trisectus Spenner	nom. incert.
var. vulgaris Spenner	= 8
"form" baudotii (Godron) Hiern	= 6
"form" circinatus (Sibth.) Hiern	= 14
"form" confervoides (Fr.) Hiern	= 12 a
"form" confusus (Godron) Hiern	= 6
"form" elongatus (F. Schultz) Hiern	= 8
"form" floribundus (Bab.) Hiern	= 8
"form" godronii (Gren.) Hiern	= 10
"form" hederaefolius (Salisb.)	
Hiern	= 1
"form" homoeophyllus (Ten.) Hiern	= 2
"form" lenormandii (F. Schultz)	
Hiern	= 2
"form" lobbii Hiern	= 4
"form" longirostris (Godron) Hiern	= 15
"form" penicillatus (Dumort.) Hiern	= 17
"form" pseudofluitans (Syme) Hiern	= 17
"form" radians (Revel) Hiern	= 10
"form" rhipiphyllus (Bast.) Hiern	= 8
"form" saniculifolius (Viv.) Hiern	= 7
"form" trichophyllus (Chaix) Hiern	= 12
"form" tripartitus (DC.) Hiern	= 3
"form" triphyllus (Wallr.) Hiern	= 8
"form" truncatus (Koch) Hiern	= 8
hydrophilus Bunge	sp. non satis
hypotrichus Turcz.	= 10
intermedius Knaf	= 8 or 10
kaufmannii Clerc	= 12
kazunsensis Makino	= 12
kochii Beurl.	= 6
x lambertii Félix	= 6 x 10
leiospermus Hartm.	= 10
lenormandii F. Schultz	= 2
var. intermedius H. Cherm	= 3

proles lutarius (Revel) Rouy & Fouc.	= 3
leontinensis Freyn	= 8
<u>lobbii</u> (Hiern) A. Gray	= 4
<u>longicapillatus</u> Sennen	= 8
<u>longifolius</u> (Rossm.) Hegi	= 10
<u>longirostris</u> Godron	= 15
<u>lusitanicus</u> Freyn	= 5
<u>lutarius</u> (Revel) Bouvet	= 3
<u>lutulentus</u> Perrier & Songeon	= 12 a
x <u>lutzii</u> Félix	= 10 x 12
<u>macranthus</u> Tod.	= 7
<u>marinus</u> (Fr.) Hartm.	= 6
subsp. <u>baudotii</u> (Godron) Hayward	= 6
subsp. <u>confusus</u> (Godron) Hayward	= 6
<u>mauritanicus</u> Pomel	= 2
<u>microtorus</u> Arv.-Touv.	= 12
<u>minutus</u> Döll	= 12
<u>nipponicus</u> (Makino) Nakai	= 10
<u>obtusiflorus</u> (DC.) Moss	= 6
<u>ololeucos</u> Lloyd	= 5
<u>omiophyllus</u> Ten.	= 2
<u>pantothrix</u> Brotero	= 10 or 12
<u>paucicarpus</u> Arv.-Touv.	= 5
<u>paucistamineus</u> Tausch	= 10 or 12
var. <u>borealis</u> Beurl.	= 12
<u>pau</u> Sennen	= 10
<u>pectinatus</u> Dubois	= 12
<u>peltatus</u> Moench	= 10
<u>peltatus</u> Schrank	= 8
subsp. <u>sphaerospermus</u> (Boiss. & Blanche) Meikle	= 9
<u>penicillatus</u> (Dumort.) Bab.	= 17
var. <u>calcareus</u> (R. W. Butcher) C. D. K. Cook	= 17 a
var. <u>vertumnus</u> C. D. K. Cook	= 17 b
<u>peucedanifolius</u> (Ehrh.) All.	= 16
<u>peucedanoides</u> Desf.	= 16
<u>petiveri</u> Koch	= 3, 6 or 8
var. <u>major</u> Koch	= 6 or 8
var. <u>minor</u> Koch	= 3
<u>phellandrifolius</u> (Schum.) Krause	= 12
<u>pomelianus</u> Debeaux	= 7
<u>porteri</u> Britton	= 12

<i>x preaubertii</i> Félix	= 2 x 5
<i>pseudoflaccidus</i> Petunn.	= 12
<i>pseudofluitans</i> (Syme) Newbould ex Baker & Foggitt	= 17
<i>pueblensis</i> W. B. Drew	sp. non satis
<i>pumilis</i> Poir.	nom. incert.
<i>radians</i> Revel	= 10
<i>reniforme</i> Desportes	= 2
<i>rhizophyllum</i> Bast.	= 8
<i>rigidus</i> Persoon	nom. incert.
<i>rionii</i> Lager	= 13
<i>rodiei</i> Maire	= 7
<i>saniculifolius</i> Viv.	= 7
<i>sedunensis</i> Rion ex Wolf	= 13
<i>x segretii</i> Félix	= 10 x 12
<i>sphaerospermus</i> Boiss. & Blanche	= 9
<i>stagnatilis</i> Wallr.	= 14
<i>submersus</i> (Gren. & Godron) Godron	= 8 or 10
<i>tenellus</i> Viv.	= 7
<i>trichophyllum</i> Chaix	= 12
subsp. <i>lutulentus</i> (Perrier & Songeon) Vierhapper	= 12 a
subsp. <i>rionii</i> (Lager) Soó	= 13
var. <i>confervoides</i> (Fr.) Rikli	= 12 a
var. <i>eradicatus</i> (Laest.) W. B. Drew	= 12 a
var. <i>godronii</i> (Gren.) Rikli	= 10
var. <i>hispidulus</i> (E. R. Drew) W. B. Drew	= 10
var. <i>radians</i> (Revel) Rikli	= 10
var. <i>rionii</i> (Lager) Rikli	= 13
<i>tripartitus</i> DC.	= 3
<i>tripartitus</i> Kittel	= 10
<i>triphyllus</i> Wallr.	= 8 or 10
<i>usneoides</i> Greene	= 15
<i>vaginatus</i> Freyn	= 17
<i>vespertilio</i> Lojac.	= 7
<i>virzionensis</i> Félix.	= 10
<i>yesoensis</i> Nakai	sp. non satis